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CONTRIBUTIONS
TO
THE STUDY OF THE DEVELOPMENT AND LARVAL FORMS OF ECHINODERMS
III

BY

TH. MORTENSEN

WITH PLATES I—XV

D. Kgl. Danske Vidensk. Selsk. Skrifter, naturv. og math. Afd. 9. Række, VII. 1.

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The present third "Contribution to the study of the development and larval forms of Echinoderms"[1] comprises the results of studies carried out during a visit to the Marine Biological Station of the University of Egypt, at Ghardaqa on the Red Sea Coast, a little South of the Gulf of Suez, in the summer of 1936.

I beg here first of all to tender my sincere thanks to the authorities of the University of Egypt, Cairo, for the hospitality offered me in placing the facilities of this excellent laboratory at my disposal, as also for obtaining permission for me to use the Egyptian research steamer "Mabahiss" for trawling and dredging in the Gulf of Suez for some days. My no less sincere thanks are due to the director of the station, Dr. CYRIL CROSSLAND, for his untiring efforts to help me in every way, meeting my — rather insatiable — requirements for material, and helping me in all practical matters. Also the assistant of the station, H. A. F. GOHAR EFFENDI, M. Sc., was ever ready with his kind help, not the least important because of the difficulty in making the sailors of the station understand what one wanted — the Arab language being not easily mastered in the course of two or three months. Last, not least, my sincere homage to Mrs. CROSSLAND, who together with her husband, the director, made me feel at home and comfortable in their fine house, which fact, combined with the success of my scientific work at the laboratory, made my visit to this Red Sea Station an unforgettable experience.

I am very much indebted to the Carlsberg Foundation for the economical support without which it would have been impossible for me to undertake this visit.

The time spent at the station was from April 18th to June 27th. Originally I had planned to come about a month earlier, but for various reasons I had to postpone the voyage a little — which was by no means a disadvantage. The essential thing for me was to find the various Echinoderms in their breeding season. Hardly anything was known about this; but as the temperature of the sea water during the winter season is some 10° C. lower than during the summer season, it was to be expected that the breeding season of most of the Echinoderms would not begin so very early. As a matter of fact I found several species to become mature only much later, e. g. *Asthenosoma varium*, *Phyllacanthus imperialis*, which will probably not have their breeding season until July—August. Still a good many species had ripe sexual products at the time of my arrival, so that there was at once enough to do. Some species, e. g.

[1] "Contributions" I—II were published 1931 in 9. Ser. Vol. IV of these Memoirs.

Tripneustes gratilla and *Echinometra Mathœi* were nearly spent, so they must have had their (first?) breeding season at least as early as the middle of April.

A problem of great interest was, how the cultures of the larvæ would stand the high salinity prevailing in the Red Sea. In this sea, with no rivers and usually several years between the rains, the strong evaporation raises the salinity, so that in the part of the Red Sea to the North of 20° N. the salinity amounts to c. 40—44 $^0/_{00}$, against the usual oceanic salinity of c. 35 $^0/_{00}$.[1] It might well be expected that in general this high salinity would not be detrimental to the larvæ, and so I found it actually to be the case. I even had the impression that this high salinity was very favourable to the larvæ; probably even a higher salinity would not be detrimental. It happened sometimes that I put some larvæ into small dishes in which water had evaporated so that the bottom was covered with salt crystals, which dissolved when new water was added. The salinity in such dishes was accordingly considerably higher than normal — but it did not seem to affect the larvæ in the least; they were swimming as actively as in normal sea-water. (I did not measure the salinity in such dishes, or undertake experiments as to how high salinity the larvæ would bear; an investigation of this problem would be of no small interest).

On previous occasions I have found it an excellent method for rearing Echinoderm larvæ to give them fresh sea-water daily, transferring them by means of a pipette to the fresh water; in this way the larvæ get access to their natural food, and usually thrive very well. As it would evidently be much easier, if one could give the larval cultures artificial food and thus the changing of water be unnecessary, I tried bringing with me samples of cultures of various food organisms for raising fresh cultures on my arrival at the laboratory. I thus brought along with me culture samples of the usual *Nitzschia closterium*, var. *tenuissima* and of *Chlorella Spärcki*, given me from the Physiological Institute of the University of Copenhagen. Further my friend Professor Brinkmann, Bergen, sent me samples of a *Chlamydomonas* sp. and a *Dunaniella* sp. Of all these four types I succeeded in raising very fine new cultures at the laboratory, in the usual way adding Miquel-solution to the filtered sea-water (cf.

[1] During the recent researches in the Red Sea of the Egyptian research vessel "Mabahiss" the hydrographer Abd el Fattah Mohamed, M. Sc., found the following salinity and P_H values at a station between Sha'b Abu Qalawa and Sha'b Abu Fanadir (in the immediate neighbourhood of Ghardaqa) on Dec. 12th, 1935:

Depth (m.)	Temperature	Salinity $^0/_{00}$	P_H
0	23.66	40.32	8.02
10	23.67	40.37	8.03
20	22.68	40.44	8.03
30	22.45	40.49	8.03
40	22.05	40.52	8.02
50	21.75	40.52	8.02

I am indebted to Dr. Crossland for this information. A report on the Hydrography of the Northern Red Sea, in which the above observations will be found included, will be published later by Abd el Fattah Mohamed.

ALLEN & NELSON. On the artificial culture of marine Plankton Organisms. J. Mar. Biol. Assoc. VIII. 5. 1910). I did not, however, find any of these cultures wholly reliable as food for the larvæ, and gradually I gave up the use thereof and returned to my old method of giving the larvæ fresh sea-water every day, or at most every few days.

This method proved completely successful[1] — but, of course, it involves considerably more work, and as I had several cultures going at the same time, and always at least three or four dishes of each culture, (— there is always the risk that, if one has only one dish of a culture, it may fail for some reason or other and thus the whole culture be spoiled; as a matter of fact, it happened often that in one or other dish the larvæ would not go on developing, whereas in other dishes, under exactly the same treatment, the larvæ were growing excellently —) work gradually increased so as to be too much for one. It was therefore a great help to me, when Professor A. NAEF of the Egyptian University, Cairo, sent his Assistant, ZAKY EL DESSOUKI, down to the laboratory to assist me in my work, from June; I am deeply obliged to Prof. NAEF for rendering me this service. ZAKY EFFENDI proved to be very able, indeed, and helped me excellently; moreover, when I left the station, he took charge of those of my cultures not yet finished — particularly *Eucidaris metularia* and *Stichopus variegatus* — reared them to metamorphosis and sent me the various stages, excellently preserved so that I could study them at home. I beg here to tender my sincere thanks to ZAKY EFFENDI for his excellent and genial help.

As for the preservation of the larvæ I found 4 $^0/_0$ formalin, neutralized with borax, to be most excellent; it preserved these delicate objects in the most perfect way, without any shrinkage, as also the skeleton was perfectly preserved. In several cases I had to kill the larvæ on the microscopical slide for drawing them, it being not desirable to press the cover so much as to keep them immovable for a camera lucida drawing. The method used was to put a drop of formalin on the slide, sucking it slowly into the water under the cover by means of a small piece of filter paper. Thus the larvæ were made immovable, in perfect shape, their colour usually remaining unchanged for some time; and then, of course, I could check all the details on the living specimens.

No special effort was made for keeping the cultures at a constant temperature; as a matter of fact the temperature of the water in the laboratory was usually somewhat lower than that of the surface water outside. But also outside the temperature varies very considerably, at least near the coast, so that also under natural conditions the larvæ are exposed to considerable changes of temperature, and it is therefore not surprising that they are not very sensible to such changes when raised in cultures in the laboratory. I kept the dishes covered with glass-plates, but so as to leave

[1] KATZUSO ONODA ("Notes on the development of some Japanese Echinoids with special reference to the structure of the larval body". Japanese Journ. of Zool. VI. 4. 1936) used with equal success a different method. To filtered sea-water was added every day a small quantity of food, collected by filtering water in which sea-weeds had been washed. The water of the cultures was not changed.

free access of air, in good light, but usually avoiding direct sun upon them; still even exposure for a couple of hours to the morning sun, involving some rise of the temperature, did not have any bad effect on them. On the whole I found the larvæ rather surprisingly resistent. I ascribe this mainly to the unusually fine condition of the sea-water at the laboratory, it being, — except when strong winds to some degree stirred up the bottom — very pure, almost as pure as in mid ocean; and then the unusually high salinity, as mentioned above, is another most important factor. Another very important factor is the high P_H value, 8.02—8.03, as stated above, p. 4 Note.

Altogether, the physical conditions for such work as that undertaken by me during my stay at the Ghardaqa laboratory are the best possible. Unfortunately the Echinoderm fauna is not particularly rich, not nearly as rich as in corresponding localities in the Indian Ocean (e. g. Mauritius) — not to speak of the Malay region, the richest region in the whole world. Of course a good number of typical coral reef Echinoderms are found, e. g. *Diadema*, *Ophiocoma*, various Comatulids — but the absence of such forms as *Astropyga*, *Echinothrix*, *Stomopneustes*, *Echinoneus*, *Archaster*, and the scarcity of a number of other forms is a regrettable fact. Probably several of these forms may be found in other parts of the Red Sea — but distances are great, which makes it difficult to get such forms alive at the laboratory for biological work. This difficulty was felt the more strongly, because the motor launch of the station was out of working order during the time of my visit. It was thus only such forms as could be found on the coral reefs close to the station and in the littoral region, and such as could be dredged by means of a small sailing boat in the immediate neighbourhood of the station at depths not exceeding some 25 fathoms, that were available for my work. In spite of this drawback I had the opportunity of studying the development of no less than 30 different species of Echinoderms — a record which by far exceeds what has been achieved anywhere else in the world by the present author or by anybody else. This is in itself proof enough of the exceptionally favourable physical conditions found at this Red Sea laboratory. As a matter of fact not one of my cultures failed — a very fortunate circumstance, since in several cases I succeeded only once in getting a ripe male and female at the same time, so that it would have been impossible to start new cultures of such species.

The species the development of which was studied are the following:

Echinoidea:

1. *Eucidaris metularia* (Lamk.), reared to metamorphosis
2. *Diadema setosum* (Leske), reared through metamorphosis
3. *Temnotrema scillæ* (Mazetti), reared to metamorphosis
4. *Nudechinus Gravieri* (Koehler), reared through metamorphosis
5. *Tripneustes gratilla* (Linn.), reared to metamorphosis
6. *Echinometra Mathæi* (Blv.), reared to metamorphosis
7. *Heterocentrotus mammillatus* (Linn.), reared through metamorphosis
8. *Fibularia craniolaris* (Leske), reared through metamorphosis

9. *Clypeaster humilis* (Leske), reared through metamorphosis
10. *Echinodiscus auritus* Leske, reared to full larval shape
11. *Lovenia elongata* (Gray), reared to full larval shape

Asteroidea:

12. *Astropecten polyacanthus* Müll. & Troschel, reared through metamorphosis
13. *Astropecten velitaris* v. Martens, reared through metamorphosis
14. *Asterope carinifera* (Lamarck), reared to metamorphosis

Ophiuroidea:

15. *Ophiothrix triloba* v. Martens, reared to metamorphosis
16. *Ophiomaza cacaotica* Lyman, reared through metamorphosis
17. *Ophiocoma erinaceus* Müll. & Troschel, reared to full larval shape
18. *Ophiocoma scolopendrina* (Lamarck), reared through metamorphosis
19. *Ophiocoma lineolata* (Desjardins) Müll. & Troschel, reared through metamorphosis

Holothurioidea:[1]

20. *Synaptula reciprocans* (Forskål), reared to full (?) larval shape
21. *Synaptula vittata* (Forskål), reared to full (?) larval shape
22. *Stichopus variegatus* Semper, reared through metamorphosis
23. *Actinopyga serratidens* Pearson, reared through metamorphosis
24. *Actinopyga mauritiana* (Quoy & Gaimard) (var.), reared to full larval shape
25. *Holothuria* (*Bohadschia*) *marmorata* Jäger, reared to full larval shape
26. *Holothuria arenicola* Semper, var. *Boutani* Hérouard, reared through metamorphosis
27. *Holothuria scabra* Jäger, reared to full larval shape
28. *Holothuria spinifera* Théel, reared through metamorphosis

Crinoidea:[2]

29. *Tropiometra Audouini* A. H. Clark, reared to young Pentacrinoid
30. *Lamprometra Klunzingeri* (Hartlaub), reared to young Pentacrinoid

Foremost in importance of these stand *Eucidaris metularia*, the first Cidarid of which we know now the full developmental history until metamorphosis, and *Diadema setosum*, the postembryonal development of this very important type being herewith made known.

The other Echinoids, the development of which has been studied here, are important in giving further proof for the correctness of my assertion (cf. my "Studies of the development and larval forms of Echinoderms", 1921, p. 201—217) that the larvæ offer a classification corresponding to the classification of the adult forms, the study of the larval forms thus affording an important test of the classification of the

[1] I am indebted to Mr. S. Heding, Zoological Museum, Copenhagen, for the identification of the Holothurians.

[2] I am indebted to my friend Professor T. Gislén, Lund, for the identification of the Crinoids.

adult forms. — I may point out the strange character of the body rods in the *Nudechinus* larva and the extraordinary beauty of the *Clypeaster humilis* larva.

It was a great disappointment to me that I did not find *Asthenosoma varium* ripe, and thus could not study the development of this important type. It will probably be ripe in July—August, since by the end of June the spermatozoa began to ripen. The fact that the spermatozoa have a very elongate head, quite unlike that of other Echinoid spermatozoa, is very interesting and indicates that the development may offer unusual features.

The Asteroids are rather poorly represented in these researches, the larvæ of only three species having been studied. This is due to various circumstances. One, *Luidia Savignyi* (Audouin), resisted all my efforts. It is a curious fact that the eggs of several Asteroids do not lend themselves directly to fertilization, such as is the case with the Echinoid eggs. When taken out of the ovaries they have a large, distinct nucleus, and are not ripe for fertilization; but when left in the water for some hours some of them will ripen, the nucleus disappearing, and such eggs are then ready for fertilization — often it is only a few percent, but by the great number of eggs even a few percent of them may yield a sufficient number of larvæ, the more so as the embryos are generally of a fair size and thus easily handled. Then comes another difficulty: that the spermatozoa are generally immovable when removed from the testes to a dish with sea-water. It is then necessary to raise the alcalinity of the water by adding NaOH; it is rather astonishing how much NaOH must be added, before the spermatozoa will move; but when this finally has been achieved, the eggs in which the nucleus has disappeared may be fertilized. (In nature such difficulties, of course, cannot exist; when the female sheds its eggs they will evidently all be ready for fertilization, and the alcalinity (P_H) of the sea-water must be high enough for the spermatozoa to move). In this way I succeeded in getting cultures of the two *Astropecten* species and of the *Asterope*; but of the *Luidia* I could not, in spite of repeated efforts, get any fertilization, and though I kept a number of them in the tanks of the laboratory, they would not shed their sexual products. Of other species I could never get ripe males and females at the same time, even though they were kept in the tanks for a long while, and others again, like *Echinaster purpureus*, the large, yolky (nearly black) eggs of which do not lend themselves for artificial fertilization, would not shed their sexual products, though kept in good numbers in the tanks. The same was the case with *Fromia monilis* (?) which, by the way, I found to be a *proterandric hermaphrodite*, this species, together with *Asterina gibbosa* (cf. L. Cuénot. Notes sur les Echinodermes. III. L'hermaphroditisme protandrique d'Asterina gibbosa Penn. et ses variations suivant les localités. Zool. Anz. 1898, p. 273) representing the only cases of normal hermaphroditism known till now among Asteroids.[1]

[1] According to H. Ohshima (Hermafrodita marstelo, Asterina Batheri Goto. Ann. Zool. Japon. 12. 1929) hermaphrodite specimens are of fairly common occurrence in *Asterina Batheri*; but the majority of the specimens are unisexual.

In Ophiuroids it seems to be a nearly constant rule that eggs taken out of the ovaries, even if they look ever so ripe, cannot be fertilized; there is always a distinct nucleus, and even when left for hours in the water they will not ripen, such as is usually the case, to a more or less extent, with the Asteroids — whereas there is never any trouble with the moveability of the spermatozoa of Ophiuroids. The only way to get the embryos of Ophiuroids is to let them spawn in the aquaria, and this, fortunately, they are not unwilling to do, when a number of ripe males and females are put together — sometimes they may spawn even in quite small dishes. In this way I got the larvæ of the five above mentioned species — the only ones of which a fair material of ripe males and females was accessible to me. — Of particular interest are here *Ophiomaza cacaotica*, the larva being of the typical Ophiotrichoid type, as should be expected according to my theory of the larval classification, and *Ophiocoma lineolata* on account of the remarkable reduction of the larval skeleton.

The Holothurians proved the great surprise! Very little work has been done on the development of such Holothurians as have pelagic larvæ, viz. the Synaptids and the Aspidochirotes. The species, the development of which has been studied from the egg onwards are: *Leptosynapta inhærens* (O. Fr. Müller), *Holothuria tubulosa* Gmelin, *H. floridana* Pourtalès, *H. Poli* delle Chiaje, *H. nigra* Peach, *Holothuria* sp., *Stichopus californicus* (Stimpson), and *St. Kefersteini* Selenka. Of these *Leptosynapta inhærens* and *Holothuria floridana* have direct development, without a pelagic larva, and none of the others have been reared to full larval shape, still less through metamorphosis. (*Labidoplax digitata* (Montagu), the classical object for studying Holothurian development, has not been reared directly; the various developmental stages have been taken pelagically).

As pointed out already by Selenka (Zur Entwicklung der Holothurien (Holothuria tubulosa und Cucumaria doliolum). Zeitschr. wiss. Zool. XXVII. 1876, p. 157) artificial fertilization of Holothurians very rarely succeeds; the eggs when taken from the ovary always have a distinct nucleus, and even when left in the water for several hours very few eggs will become ripe for fertilization, so that it is very difficult to get larval cultures in this way. By means of keeping a number of specimens in a live-box Selenka succeeded in getting good cultures of *Holothuria nigra*, and Edwards of *Holothuria floridana*, the specimens having spawned in the live-box. Only Hörstadius (Entwicklungsmechanische Studien an Holothuria Poli d. Ch. Arkiv för Zoologi. 17. B. 1925) has succeeded in getting a large number of eggs artificially fertilized, having raised the P_H of the water. Perhaps this method will prove successful also in other difficult cases.

At Ghardaqa Holothurians are plentiful, several species being quite common in shallow water at the station. On keeping a number of specimens (each species separate, of course) in the tanks of the laboratory, where they would live quite well for some days, though without food, I had the pleasure of seing some of them spawn. Particularly *Holothuria marmorata* was very interesting to observe in the act of spawning. First a male would raise its foreend almost vertically, spreading it out behind the tentacles and flattening it so as to recall, indeed, a cobra in attacking position; a distinct genital papilla would appear, from which the sperma would stream, forming a milky cloud in the water. Then a female would raise its foreend in the same way and shed its eggs. Several specimens might be seen spawning at the same time. Particularly the males would move the raised foreends to the sides, thus producing a better spreading of the sperma in the water. When the spawning had ended they assumed their normal horizontal position. The spawning usually took place in the evening or the night.

The eggs thus spawned naturally I always found immediately fertilized, and I could then remove the eggs from the bottom of the tank by means of a pipette and put them into dishes with pure water. In some cases, when I did not directly observe the spawning, and the eggs were not numerous enough to be sucked up from the bottom of the tank, I filtered all the water from the tank through a fine net of silk gauze and thus got the eggs removed to dishes with fresh sea-water.

In this way I got larval cultures of all the 9 species of Holothurians named in the above list. Some species would, however, not spawn, though they were apparently ripe. I tried then to fertilize the eggs artificially, but in spite of repeated efforts, always without success.

All the cultures obtained in the way described proved perfectly successful, the larvæ reaching their full shape, and four of the species, the *Stichopus*, *Actinopyga serratidens*, and two of the *Holothuria* species even metamorphosed. The larvæ were found to be extraordinarily uniform in shape and colour, so as to be distinguishable only by the calcareous bodies in their posterior end. But then I was surprised to find the larvæ, when about to begin metamorphosing, to develop in their lobes large, clear, elastic balls, these balls remaining distinct also in the young Holothurian after metamorphosis.

This recalls the observations of Joh. Müller in his II., III., IV., and VI. "Abhandlungen über die Larven und die Metamorphose der Echinodermen" 1848—1853. He there describes and figures excellently some "Holothurienlarven mit Blasen", the metamorphosis of which into young Holothurians he has followed in details on material taken pelagically. Nobody has observed these peculiar larvæ since Joh. Müller studied them nearly a hundred years ago, and it was quite problematic to which Holothurian they belonged, the suggestion of Joh. Müller that they might be the larvæ of *Stichopus regalis* being quite uncertain (and, indeed, as it now appears, incorrect). In my "Echinodermenlarven d. Plankton-Expedition" (1899, p. 19) I named them *Auricularia sphærigera* and *A. stelligera* finding the figures given by Joh. Müller to represent two distinct species of larvæ. It is now made certain that they belong to the genus *Holothuria*, and as the *Stichopus* larva has the same sort of elastic balls, it seems evident that we have here a larval type characteristic of the *Aspidochirotes*. That such balls were not found in the above mentioned *Holothuria* and *Stichopus* species, the development of which was hitherto studied, is due to the fact that the balls do not appear until the larva is fully formed and ready to metamorphose, whereas only the young stages of the larvæ of the said species were reared.

The two Comatulids of which the development was studied, did not present any external features of special interest, the development agreeing in all essential features with that of *Tropiometra carinata*, as described in my "Studies on the development of Crinoids" (Papers from the department of Marine Biology, Carnegie Inst. XVI. 1920). But it is important that in both of them the eggs are free, not attached to the pinnules, this latter mode being apparently a secondary adaptation for protection of the brood, the principal and probably the commonest mode being that of the eggs being free. *Lamprometra* offers the very remarkable feature that no gastrula-invagination takes place, the stomach differentiating secondarily in the mass of cells filling up the blastula.

The main object of these researches was to make known the larval forms of the various species of Echinoderms available, with regard especially to their importance for classification. The same point of view has been the leading principle in my former investigations in Echinoderm development (cf. my "Studies of the development and larval forms of Echinoderms" 1921, and my "Contributions to the study of the development and larval forms of Echinoderms" I—II. 1931). Of course, I do not mean to say that with these researches we have gained sufficient information of the divers forms studied, even when the development is traced from the egg to full larval shape and through metamorphosis. The whole question of the organogeny is left nearly untouched — not because it does not interest me, but because it would involve much more work than one man could do. Each of the species dealt with might deserve a full monographic treatment, and most interesting results would be sure to be achieved thereby. But that was not my purpose, and will not be for my future researches either, if I may have the good fortune of continuing these studies. The study of the larval forms alone is a most important (and fascinating) work, and very much remains to be done in this field; we are only just so far that we can see a glimpse of what can be achieved.

In my "Studies" 1921 I gave a short summary of what had hitherto been achieved in the knowledge of the development and larval forms of Echinoderms up to 1921, and in the "Contributions" I—II. I did the same for the period 1921—1931. It may be practical here to summarize likewise what has been done in regard to this subject in the time from 1931 till now. Nearly all of it relates to the Echinoids.

Martin W. Johnson in his "Notes on the larval development of Strongylocentrotus franciscanus" (Publ. Puget Sound Biol. Station. VII. 1930) figures the various stages of this larva, which he has reared till beginning metamorphosis, thus ascertaining that the larva figured Pl. IX. Fig. 4 of my "Studies" and referred to *Strongylocentrotus franciscanus* really belongs to this species (The younger stages figured Pl. IX. 1—3, I had reared). We thus have now a fairly complete knowledge of the larval development of this species.

Mary M. Moore in "Notes on the development of the sea-urchin Temnopleurus hardwickii" (Sci. Rep. Tôhuko Imp. Univ. 4. Ser. Biology. VIII. 1933) figures the larva of this species, evidently without knowledge of the literature on Echinoderm larvæ. The larvæ are figured upside down, and only outline figures, without the skeleton, are given of the larva about to metamorphose; but of the younger stages good figures are given, showing this larva to be of the usual Temnopleurid type.

Amado T. Feliciano ("Studies on the early development of Arachnoides placenta (Linn.). Natural & Applied Sci. Bulletin Univ. Philippines. III. 4. 1933) describes and figures, rather crudely, the larva of this species; from his Pl. II. Figs. 23, 24 it can be concluded that it must be very much like the larva of *Arachnoides zelandiæ* Gray, described and figured in my "Studies" 1921, p. 96, Pl. X. 7 (under the name of *Arachnoides placenta*, as it was at that time generally assumed, on the authority of A. Agassiz, that the New Zealand form was identical with the Indo-Pacific *A. placenta*; in my paper on the Echinoderms of New Zealand and the Auckland—Campbell Isl. I. Echinoidea (Papers from Dr. Th. Mortensen's Pacific Expedition. 1914—16. VIII. Vid. Medd. Dansk Naturh. Foren. Bd. 73. 1922, p. 180) I showed it to be quite a distinct species, as had, indeed, already been pointed out by Lovén).

Much more important than the three above mentioned papers are those of Katsuzo Onoda. In his "Notes on the development of Heliocidaris crassispina, with special reference to the structure of the larval body" (Mem. Coll. of Sci. Kyoto Imp. University. Ser. B. VII. 1931) he gives a very elaborate description and figures of this larva in all its stages and of the metamorphosis and the young sea-urchin. (The larva of this species was, however, already described in my "Studies" 1921, p. 64, Pls. VI. 3; XI. 1—2, though under the erroneous name *Heliocidaris tuberculata* (Lamk.); cf. my paper quoted above on the Echinoidea of New Zealand and the Auckland—Campbell Isl., p. 174. Note). — Further in 1936, in his "Notes on the development of some Japanese Echinoids, with special reference to the structure of the larval body" (Japanese Journ. of Zoology. VI. 4) Onoda describes and figures excellently the larvæ of *Mespilia globulus*, *Echinometra Mathæi*, *Toxopneustes pileolus*, *Echinostrephus moralis* (sic! for *molaris*), *Temnopleurus teoreumaticus*, *Tripneustes gratilla*, *Diadema setosum*, *Strongylocentrotus pulcherrimus*, and *Pseudocentrotus depressus*, that of *Echinostrephus* being entirely unknown up till then, the others being more or less completely known (cf. my "Studies" 1921). The postembryonal development of *Mespilia globulus* is very carefully described. The larva of *Echinostrephus* is shown to be of the Echinometrid type, a fact of importance for judging of the classification of this aberrant type.

Finally R. Gopala Aiyar has given a very fine and elaborate account of the "Early development and metamorphosis of the tropical Echinoid *Salmacis bicolor* Agassiz" (Proc. Indian Acad. Sci. I. 1935). He has not only reared the larvæ from the egg through metamorphosis, but also succeeded in keeping the young sea-urchins in the laboratory for a year, evidently showing normal growth.

Mention may also be made of a paper by M. Kume on the development of the Echinoids of Misaki, 1929, in the Japanese Journal of Zoology, No. 41. It is wholly in Japanese, and thus wholly closed to me. But a couple of figures, one of *Strongylocentrotus pulcherrimus*, the other of *Pseudocentrotus depressus* are valuable, the latter having been reared a little further than it was reared by ONODA, though still not nearly to full larval shape.

Nothing has been done on the larval development of Asteroids or Crinoids, but on Ophiuroids important observations are made by GUNNAR THORSON and by NARASIMHAMURTI. In his paper "On the reproduction and larval stages of the brittle-stars Ophiocten sericeum (Forbes) and Ophiura robusta Ayres in East Greenland (Medd. om Grønland. Bd. 100. 4. 1934) THORSON describes the larvæ of these two Ophiuroids, which he has been able to identify from the plankton catches. Particularly the *Ophiocten* larva is interesting in having a recurrent rod, a fact not helping to solve the difficult problem of the Ophiolepidid larvæ.

NARASIMHAMURTI has published an important paper on "The development of Ophiocoma nigra" (Qu. Journ. Micr. Sci. 76. 1. 1933), in which the whole larval and postembryonal development is elaborately described. Evidently NARASIMHAMURTI did not know anything of what was previously known about the development of this Ophiuroid; that the larva was figured by GRAHAM KERR 1912 (The Glasgow Naturalist. IV); that fertilization was made by me at the Plymouth laboratory and the first development stages described in my paper "On the development of some British Echinoderms" (J. Mar. Biol. Ass. X, p. 12); that the nervous system of the larva was represented in my "Notes on the development and the larval forms of some Scandinavian Echinoderms" Vid. Medd. Dansk Naturh. Foren. 71. 1926); that the larva was figured and described in my "Handbook of the Echinoderms of the British Isles" 1927, p. 178; and in my "Contributions to the study of the development and larval forms of Echinoderms" I—II. (Mem. Acad. Copenhague. 9. Ser. IV. 1931, p. 34. Pl. IV. 1), all these papers being represented in the library of the Plymouth station, where he reared the larvæ.

Finally may be mentioned the discovery of viviparity in a great number of mainly Antarctic Ophiuroids, as set forth in my Report on the Echinoidea and Ophiuroidea of the "Discovery" Expedition (Discovery Reports, Vol. XII. 1936). The whole subject of the viviparity, and the therewith connected hermaphroditism, is dealt with there, pp. 204—208. To enumerate here all the new cases of viviparous Ophiuroids I think superfluous; it may suffice to refer to the said work.

As for the Holothurians I may recall the fact (overlooked in my "Contributions" of 1931) that HÖRSTADIUS (Op. cit. 1925) has reared the larva of *Holothuria Poli* d. Ch.; he does, however, not describe or figure this larva, which is thus still unknown.

Echinoidea.

1. **Eucidaris metularia** (Lamarck).

Pls. I—II.

Specimens of this species — which is not common at Ghardaqa, apparently occurring only on the outer reefs — were not found to be ripe until early in June. A number of specimens were kept in the tanks of the station, where they lived quite well for some time. On June 4th some specimens were found to have ripe sperma, but no specimens to have ripe eggs. Then the next day a number of females had the eggs perfectly ripe — as if on command! (I had formerly found this species ripe early in April at Hawaii; cf. my "Studies of the development and larval forms of Echinoderms", 1921, p. 24). Fertilization was thus undertaken on June 5th, and proved perfectly successful.

The eggs are small, c. 0.09 mm., quite clear. The fertilization membrane lies so close to the egg-surface as to be almost indiscernible; only at the first cleavage stages it becomes discernible across the notch between the cleavage cells. Already after 6 hours the embryos are beautiful blastosphæras, very clear, and about twice the size of the egg, the cells being very low (Pl. I. Fig. 4). The cells, the limits of which are very distinct, are rather unequal sized; I have, however, been unable to discern any distinct difference in the size of the cells in the first cleavage stages (Pl. I. Figs. 2—3); also I find the number and distribution of the larger cells rather variable, so it would seem that no great importance attaches to this difference in the size of the cells in the blastosphæra.

At the age of about 24 hours the gastrula-stage has been reached. The archenteron is remarkably slender and elongate; a conspicuous proliferation of mesenchyme cells takes place at the upper end of the archenteron (Pl. I. Fig. 5). At this stage the limits of the ectoderm cells are still quite distinct; in the following stage of the development these cell limits are no longer discernible.

Whereas the young gastrula is still almost spherical, like the blastosphæra, the shape changes very markedly in the course of the next 24 hours into an almost triangular, flattened form (Pl. I. Fig. 6). The proliferation of the mesenchyme cells gradually stops, and the upper end of the archenteron widens, evidently for the formation of the mesoderm pouches (which I have not directly observed, however). At the same time the archenteron curves dorso-ventrally, its upper end meeting an ectodermal invagination, the larval mouth, and the ventral surface of the embryo becomes somewhat sunken round the mouth.

At the age of four days the embryo begins to assume the larval shape, and the first rudiments of the skeleton appear (Pl. I. Fig. 7). The larva at this early stage closely resembles that of *Eucidaris tribuloides*, as figured by Tennent in his "Studies of the hybridization of Echinoids, Cidaris tribuloides". (Publ. No. 312 of the Carnegie Inst. Washington, 1922, fig. 4, p. 10). Its nearly horizontally directed postoral processes suggest that it will develop into a form with long horizontal arms like the

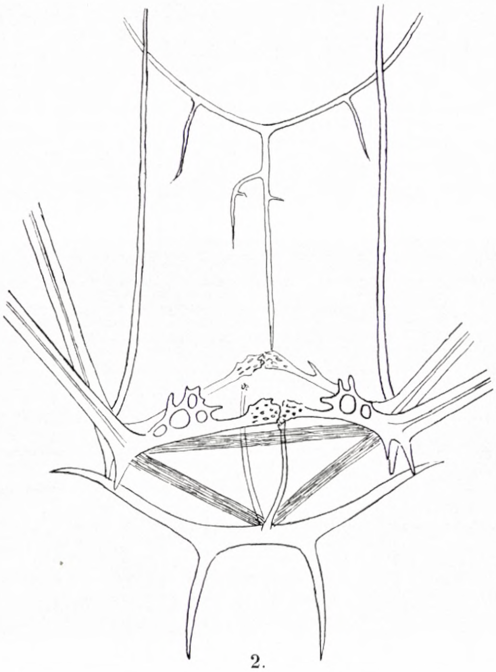
Diadema larva, the *Echinopluteus transversus*, as, indeed, I formerly thought the conclusion inevitable that *Echinopluteus transversus* must be a Cidarid larva (cf. my "Studies of the development and larval forms of Echinoderms", 1921, p. 251). Even after I had proved the larva of *Diadema* to be the *Echinopluteus transversus*, I still thought the young larva of *Eucidaris tribuloides* figured by TENNENT (Op. cit.) to prove that the Cidarid larvæ must belong to the same larval type, although "it would

a. b.

Fig. 1. Skeleton of the larva of *Eucidaris metularia* (Lamk.). a. From a larva three weeks old, with posterodorsal rods, dorsal arch, and posterior transverse rod. b. The postoral rod of a larva 9 days old, showing the very small and distant holes of the fenestrated rod; from the anterolateral rod proceeds a rudimentary recurrent rod; body rod short, rudimentary. × 290.

be highly remarkable to find in two so widely different families as the Cidaridæ and the Diadematidæ the same highly specialized larval type" (cf. my "Contributions to the study of the development and larval forms of Echinoderms", I—II, p. 17). Also the young larva of *Eucidaris Thouarsii*, figured in my work quoted of 1921, Pl. V. 2, points in the same direction. It was therefore with great excitement that I watched the further development of the *Eucidaris metularia* larva, expecting now finally to get the solution of the perplexing problem offered by the Cidarid larval type. In the course of a few days it became clear that this larva would not develop into a form like the *Echinopluteus transversus*. As seen in Pl. I. Fig. 8, representing a larva 9 days old, the postoral arms gradually become more upwards directed, the shape being now more of the usual type of young Echinoid larvæ.

Characteristic of the young larva is the very slight development of the body skeleton. There is no basket structure, the body rods being quite short, and there is only the merest indication of a recurrent rod, this being even not of constant occur-



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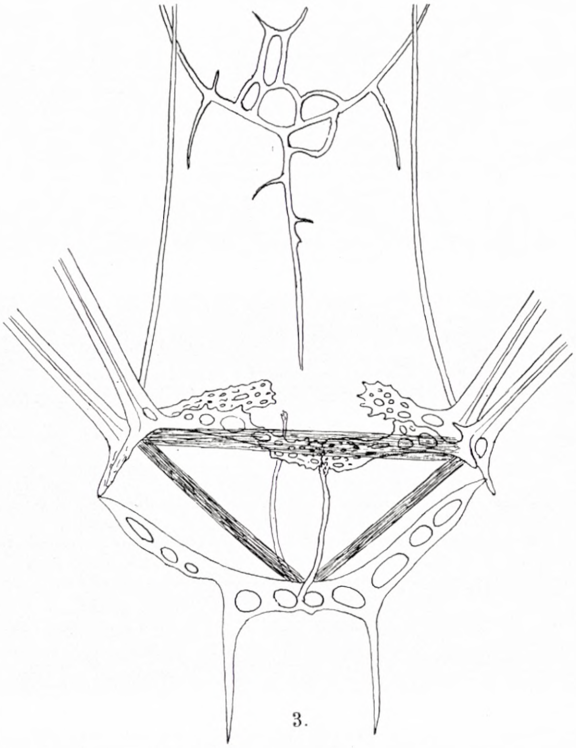
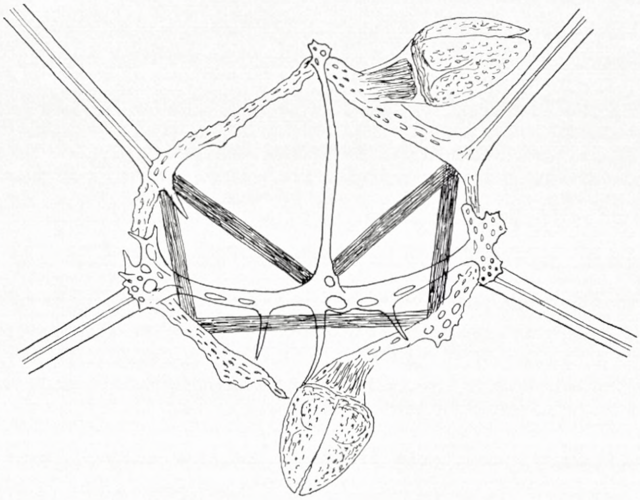


3.

Figs. 2—3. Skeleton of fully formed larva of *Eucidaris metularia* (Lamk.), 3. slightly older than 2., as appears from the more complicate posterior transverse rod and dorsal arch. The dark bands in these figures, and in fig. 4, represent the larval muscular system. × 215.

rence. The postoral rod is of the fenestrated type, but the holes are not distinct till a good distance out; they are at first very small and distant, farther out they are gradually larger and closer together. The rod is perfectly smooth (fig. 1, b; fig. 5, c, d). The anterolateral rod is simple, entirely smooth, as is the whole skeleton. Anterolateral arms are only indicated; the frontal lobe is high and arched, and the whole body unusually broad and swollen, but perfectly clear and transparent, apart from some few, scattered crimson pigment spots; also some peculiar clear balls are found in the end of the postoral arms. The suboral cavity is very conspicuous, as was also the case in the younger stages.

At the age of three weeks the larva had assumed the shape shown in Pl. I. Fig. 9. Posterodorsal arms have appeared, but they are still only short; the posterodorsal rod is fenestrated like the postoral rod. Posterolateral lobes have begun to form, and a pair of conspicuous postoral vibratile lobes have formed, whereas the corresponding dorsal lobes are still indistinct. The corners of the postoral lobe are markedly produced, whereas the anterolateral arms are still merely indicated. The dorsal arch



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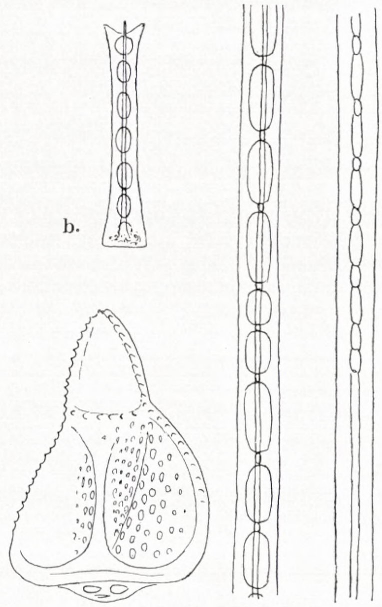


5.

Fig. 4. Skeleton of a larva in beginning metamorphosis, seen half from behind. Two pedicellariæ have appeared. × 215.

Fig. 5. a. Valve of globiferous pedicellaria; b. embryonal spine; c—d. parts of the postoral (or posterodorsal) rod, c. from the basal, d. from the distal part, showing the characteristic difference in the size of the holes. a, c, d. × 430; b. × 240.

has been formed, but has not yet developed far enough to provoke the formation of preoral arms. The first rudiment of a posterior transverse rod is seen (fig. 1, a). There is a conspicuous spot of crimson pigment at the point of the long arms, as also in the lobes, and scattered small crimson spots are found all over the body.

So far the *Eucidaris* larvæ had reached in their development by the time I had to leave the station. Fortunately my assistant, Zaky Effendi, could go on looking after the larvæ, and in the samples later on received from him I found the fully formed larvæ up till beginning metamorphosis, in perfect state of preservation. Only about the colour of the fully formed larvæ there is no information, beyond the fact that these larvæ, as preserved in Canada balsam, show the intestine strongly pigmented with light brownish spots.

The fully formed larva is particularly characteristic by its numerous large ciliated lobes. Not only has it the usual posterolateral, postoral and posterodorsal lobes, but there is also a pair of anterodorsal lobes, and the anterior corners of the postoral area have been produced into a pair of lobes corresponding to the anterodorsal ones (Pl. I. Fig. 10; Pl. II). Anterolateral and preoral arms are well developed, though not very long, particularly in comparison with the very long postoral and posterodorsal arms. These latter, which are slightly widened at the base, must be actively movable, as evinced by the well developed muscular system connecting their bases (figs. 2—4). The posterodorsal rod is exactly like the postoral one.

In the skeleton the most characteristic part is the posterior transverse rod. It is gracefully curved and has a pair of strong thorns, directed backwards; from the middle of it proceeds a long ventral and a dorsal median process, which reach up to the ventral and dorsal transverse rods (figs. 2—4). In the later stages some meshwork develops along the posterior edge of the posterior transverse rod, and its ends, as well as the ends of its median processes, develop into fenestrated plates. At the same time the ventral and dorsal transverse rods — which are originally simple, slender rods — develop into fenestrated plates, which form a conspicuous calcareous ring around the posterior end of the body (fig. 4). In this ring also takes part the body rod and an inconspicuous prolongation from the posterodorsal rod; but these parts are evidently of much less importance than the transverse rods. On these widened transverse rods the first pedicellariæ and spines appear; further a pedicellaria develops on the dorsal arch, which likewise develops into an irregular, fenestrated plate (figs. 3—4). It may be added that at the stage, where the first pedicellariæ and spines have appeared, also the first tubefeet have been formed; but the details, particularly the formation of the plates of the test could not be followed on the material available. It is clear, however, that the widened transverse rods and dorsal arch represent the five genital (basal) plates (cf. v. Ubisch. Anlage u. Ausbildung d. Skeletsystems einiger Echiniden. Zeitschr. f. wiss. Zool. CIV. 1913. Taf. VII; I. Gordon. Skeletal development in Arbacia, Echinarachnius and Leptasterias. Phil. Trans. B. 217. 1929; Onoda. Notes on the development of some Japanese Echini. Japanese Journ. of Zool. VI. 1936). The ocular plates have not yet been formed at this stage.

The pedicellariæ are recognizable already as of typical Cidarid structure, of the small globiferous type (fig. 5, a).

Having thus traced a Cidarid larva to its final shape we see that there is no real resemblance between the Cidarid and the Diadematid larval type, the remarkable resemblance between the young Cidarid larva and the fully formed Diadematid larva, the *Echinopluteus transversus*, being merely a curious coincidence of no real morphological value — judging from the very few larvæ hitherto traced with full certainty, viz. the *Diadema* and the *Eucidaris* larvæ. But there are two other larvæ to take into consideration here, viz. the larva of *Dorocidaris papillata* (= *Cidaris cidaris* L.), and the larva figured by Joh. Müller on Taf. V. 1—3 of his VII. Abhandlung über die Metamorphose der Echinodermen (Abh. d. Akad. Berlin, 1855).

The larva of *Cidaris cidaris* was studied very carefully by PROUHO in his "Recherches sur le Dorocidaris papillata" (Arch. Zool. Exp. et Gén. 2. Ser. V. 1888, Pls. XXIII—XXV). The youngest stages differ rather conspicuously in shape from those of *Eucidaris*, and also the last stage figured by PROUHO (Pl. XXV. 2) is conspicuously different from the final shape of the *Eucidaris* larva; but evidently PROUHO did not succeed in rearing his larvæ to the final stage, as may be concluded from the fact that the posterior transverse rod is represented as quite small. As a matter of fact this larva is only slightly older than the stage of the *Eucidaris* larva represented here in Pl. I. Fig. 9. This fact, combined with the very different mode of drawing (— artistically PROUHO's figure is far beyond my drawings —) makes out for the differences, and it seems certain enough that the *Cidaris* (*Dorocidaris*) larva belongs to the same type as the *Eucidaris* larva, characterised, besides by the strong development of the vibratile lobes, by the faint development of the body skeleton, which does not form a basket structure.

The larva of JOHS. MÜLLER, which I designated in my "Echinodermenlarven d. Plankton-Expedition" 1898, p. 79, by the name *Echinopluteus Mülleri*, was thought by JOHS. MÜLLER to belong either to *Cidaris* or *Diadema*. Finding it to differ too much from the *Cidaris* larva as figured by PROUHO, I concluded that it would belong to *Centrostephanus longispinus*, the only Diadematid found in the Mediterranean. At that time it was also generally accepted that there was only one Cidarid in the Mediterranean, *Stylocidaris affinis* being regarded as identical with *Cidaris cidaris* (*Dorocidaris papillata*). The perfect resemblance between this larva of JOHS. MÜLLER and the fully formed *Eucidaris* larva makes it practically certain that the former is also a Cidarid larva, either of *Stylocidaris affinis* or of *Cidaris cidaris*, the two only species of Cidarids occurring in the Mediterranean — to which of the two species the larva belongs cannot be decided, because of the different character of JOHS. MÜLLER's and PROUHO's drawings, and of the different age of the larvæ represented by the two authors. Further it may now be concluded almost with certainty that the larva figured on Pl. V. 7 of my "Studies" (1921) which I referred (Op. cit., p. 29) with some little doubt to *Astropyga pulvinata* — "be it not *Eucidaris Thouarsi*, which I would not think very probable, judging from the shape of the young larva reared" (viz. on account of its horizontal arms), is in reality the larva of *Eucidaris Thouarsi*.

The rather certain demonstration of the said larva of JOHS. MÜLLER being a Cidarid larva, and that my quite similar larva from the Gulf of Panama is the *Eucidaris Thouarsi* larva, indicates that there is a larval type peculiar to the family of the Cidarids, characterised by the strong development of the vibratile lobes and by the rudimentary condition of the body skeleton. Of course this has to be corroborated by the study of the development of other Cidarids; but for the present evidences point in this direction.

The removal of JOHS. MÜLLER's larva from the Diadematids (*Centrostephanus longispinus*) does away with another difficulty, viz. the remarkable difference between the supposed *Centrostephanus* larva and the *Diadema* larva (*Echinopluteus transversus*).

It would, indeed, be just as remarkable to find within the same family larvæ so different as the *Echinopluteus transversus* and the *Echinopluteus Mülleri*, as it was to find the *Echinopluteus transversus* larval type within the two widely different families of the Cidaridæ and the Diadematidæ, both of these alternatives equally irreconcilable with the fact that otherwise we find the Echinoid larvæ grouping themselves into well marked "families" corresponding to the families of the adult Echinoids — the Temnopleuridæ, the Echinidæ, Clypeastridæ, Spatangidæ, etc. By the removal of the *Echinopluteus Mülleri* to the Cidarids the apparent non-conformity of the larvæ within the family of the Diadematidæ disappears, and we may reasonably expect that the divers genera of the Diadematids will prove all to have larvæ of the *Echinopluteus transversus*-type, as already indicated by the fact that we know quite a number of different "*Echinopluteus transversus*", as shown in my "Studies of the development and larval forms of Echinoderms", pp. 78—95. But that is for future researches; till now we know for certain only the larva of the genus *Diadema* itself.

2. **Diadema setosum** (Leske).

Pl. IX. Fig. 1.

A single ripe female and some ripe males were found on the 9th of May; but the great majority of the specimens were still unripe at that time, the 9th being two days after fullmoon. Also later on I found in general only very few specimens ripe at a time, and not specially at full moon, so that I could not confirm the observations of Munro Fox on a lunar periodicity in the reproduction of this species (Proc. R. Soc. B. Vol. 95, 1923, p. 525—530). However, this may be due to the breeding season of this species being mainly later on in the summer (Munro Fox found the largest percentage of mature specimens in July, the number being smaller in August and very small or nil in September), so that it would be exceptional to find mature specimens earlier in the summer.

Fertilization was thus undertaken on May 9th. The development proceeded as described in my "Contributions to the study of the development and larval forms of Echinoderms" I. 1931, p. 11—17, Pls. I, II. 1—3; there is no reason for giving here again a detailed description. It took a little longer for the larvæ to reach the second, the *Echinopluteus transversus*-stage, than I had found it to be the case at Onrust, viz. nearly three weeks against only two weeks at Onrust, in the Java Sea.

By my researches at Onrust I did not succeed in rearing the larvæ till beginning metamorphosis, and thus the skeleton of the second larval stage had not yet reached its full shape in my oldest larvæ; still, I thought it probable that this larva would be identical with the *Echinopluteus transversus, species f.* (from the Bay of Bengal and off the Maldive Islands) described in "Studies of the development and larval forms of Echinoderms", p. 91, Pl. XIII. 3—4. The larvæ in beginning metamorphosis from my Red Sea investigations in general bear out this suggestion. The skeleton is alike in both, as is also the general shape. It is, however, noteworthy that the length of the arms appears to be smaller than in the *Echinopluteus transversus, species f.*; in none of the specimens reared at Ghardaqa did the arms reach a greater length than 5 mm., whereas in the said sp. f. the best of the incompletely preserved arms was 6 mm., so that the complete arm would be sure to be a good deal longer, even if perhaps not so long as in the West Indian species, 12 mm. This shorter arm length in the Red Sea larvæ may perhaps be due to the artificial rearing in small dishes; unfortunately I did not succeed in catching even a single one of the larvæ in pelagic hauls by day or night, so there were no means of comparing my artificially reared larvæ with such as were reared in nature. The possibility remains, therefore, that the said species f. from the Indian Ocean belongs to *Diadema Savignyi* (or perhaps to some other Diadematid). In the larvæ reared at Onrust the arms did not surpass 2 mm. in length, but they did not reach so far as the beginning of metamorphosis, so it is rather safe to say that the arms had not grown to their normal full length. Onoda, who has reared the larva of *Diadema setosum* (Op. cit. p. 648, Pl. XIII. Fig. 11) does not say anything about the length of the arms in his larvæ; judging from the figure quoted they were not longer than in my larvæ from Onrust, and like these latter his larvæ were not near metamorphosis, so, evidently, they had not reached the normal full arm length.

As regards the shape of the larval body it may be mentioned that the vibratile band on the dorsal side makes a conspicuous downward bend so as to form a pair of dorsal lobes. The complete resorption of the anterolateral arms, combined with the widening on the middle of the dorsal side, gives the larval body a very unusual shape, as shown in Pl. IX. Fig. 1.

With beginning metamorphosis the long arms become somewhat narrower and gradually shorter — evidently, they become completely resorbed, and the calcareous material in the long rods used in the formation of the body skeleton. I have, however, directly observed only the beginning resorption of the long arms; but it is clear that they cannot be thrown off (such as is the case with the long arms in the *Ophiothrix* larvæ), since their basal part enters into the composition of the skeleton of the sea-urchin.

In larvæ near metamorphosis, when swimming, the primary tubefeet are extended to a considerable length; it looks as if they were fumbling for something to attach themselves to — and this probably is actually the case. I did, unfortunately, not observe this until just before my departure, so there was no time for further observation or for making a drawing of the larva with its extended primary feet.

When I left Ghardaqa, the larvæ, which were now 6 weeks old, were near metamorphosis, and one of them had just metamorphosed. I took then a number of the best larvæ along with me, in a jar with sea-water and a few algæ, hoping that I might thus succeed in getting some more of them metamorphosed. Although I had no sort of laboratory facilities onboard the ship, and no microscope, but only a pocket lens, I actually succeeded in getting some few more young sea-urchins in more advanced stages, so that I can here give some information of the postembryonal development of this important Echinoid type.

The newly metamorphosed sea-urchin is represented in fig. 6, seen from the aboral side. Parts of the larval skeleton are seen to develop into the genital plates, much as we know it from other Echinoids. The posterior transverse rod can be recognised, carrying a pedicellaria; also the basal part of one of the long postoral rods is seen. A third large plate, also carrying a pedicellaria, is likewise developing from part of the larval skeleton, very probably the rudimentary dorsal arch. The two other genital plates are new formations. The basal part of the second postoral rod is seen lying above one of the oculars, possibly the ocular is developing in connection

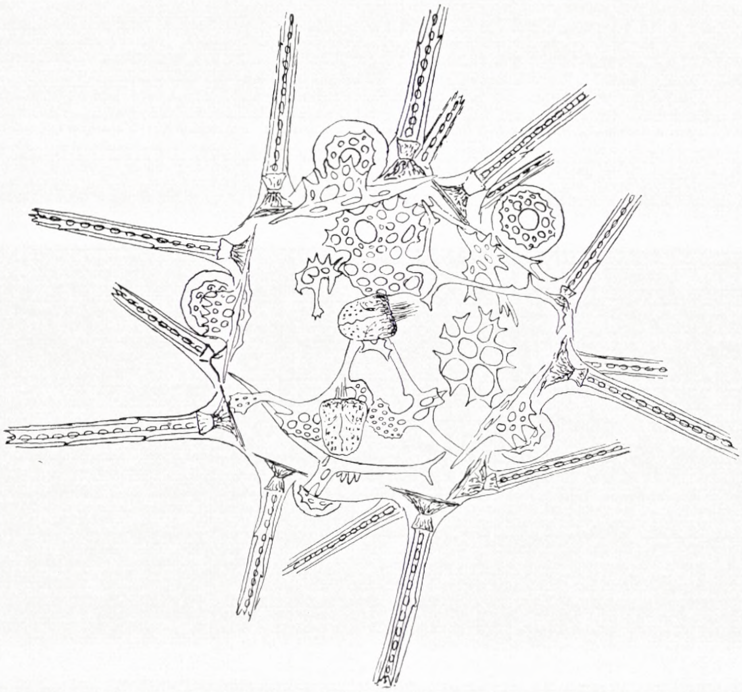


Fig. 6. Young *Diadema setosum*, newly metamorphosed. Aboral side. × 100.

with it — this I have been unable to ascertain. The oculars are peculiar in having an erect superstructure, recalling the tables of the Holothurians; this serves to recognise the ocular plates also in the later stages.

On the oral side are seen the rudiments of the five pairs of buccal plates, all equally developed. No traces of the masticatory apparatus are seen as yet, and the mouth is still closed (fig. 8). In the interambulacra the first five plates have been formed (fig. 7); it is very important that there is no trace of the plate No. 4 having originally been situated in the midline of the interambulacrum, such as is figured by Gordon for *Psammechinus miliaris* (cf. I. Gordon. The development of the calcareous test of Echinus miliaris. Phil. Trans. B. 214. 1926, p. 282).

Rather plate 5 is nearer the median line, but I do not see in the following stages any sign of its being in a median position. It is noteworthy that the plate 1, the primordial plate, is remarkably small, and its spine less developed than those of the following plates, which might indicate that it is not the first to be laid down — but this cannot be ascertained from the single specimen available of this stage. — Only the first pair of ambulacral plates have appeared. The sucking disk of the primordial tubefoot

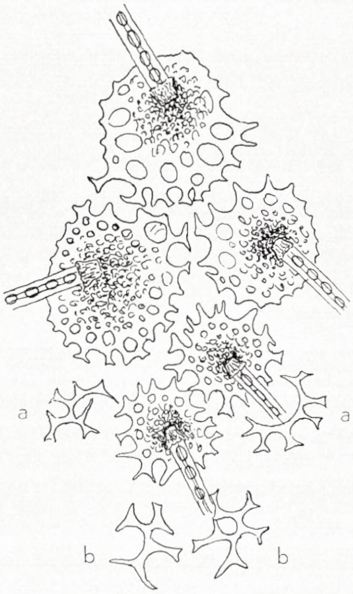


Fig. 7.

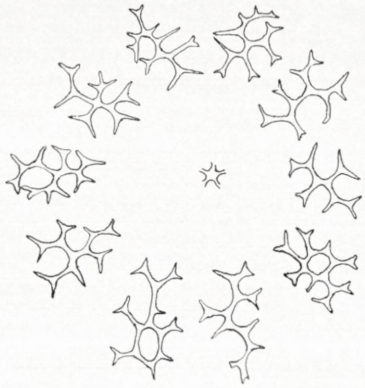


Fig. 8.

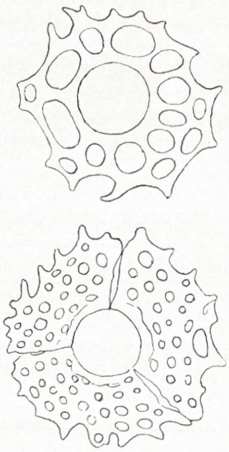


Fig. 9.

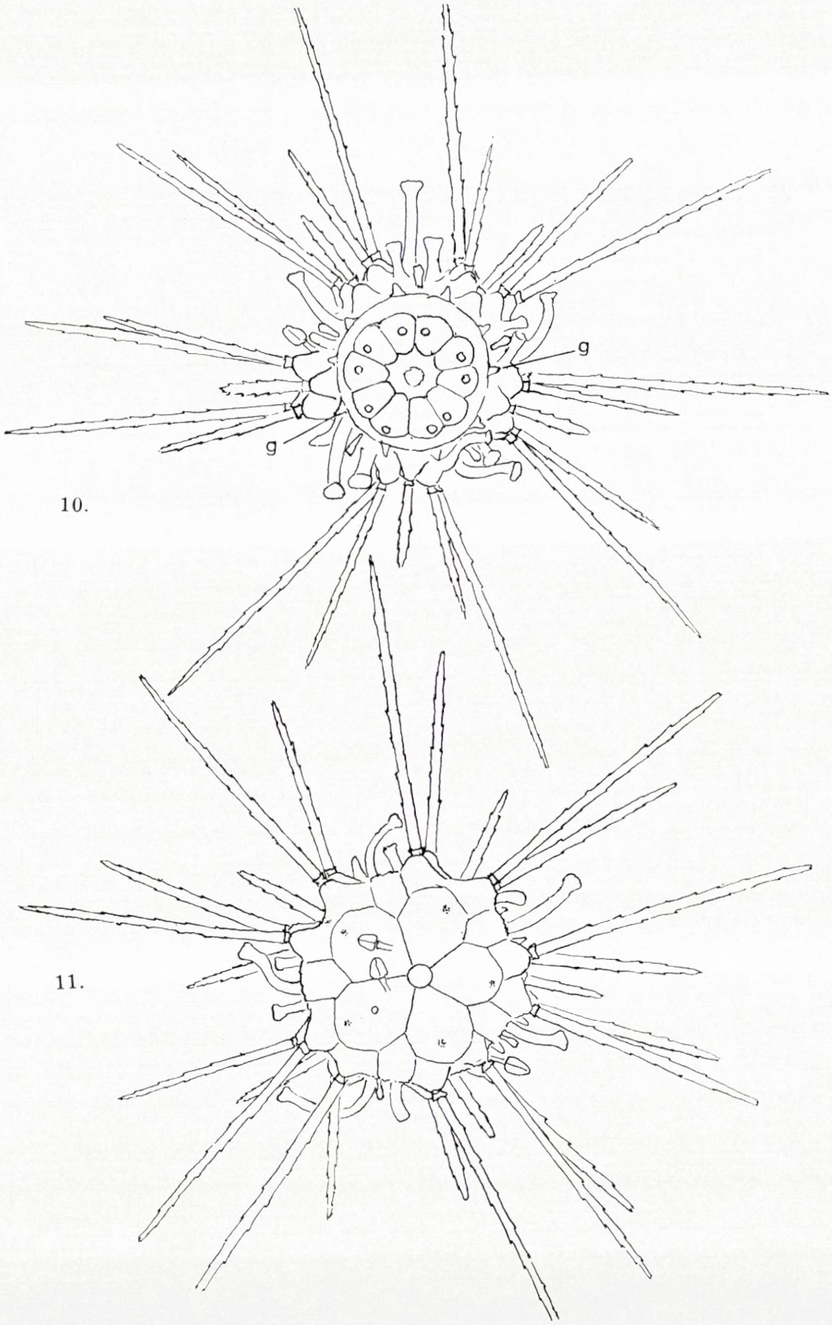
Fig. 7. Interambulacral plates of newly metamorphosed *Diadema setosum*; the lowermost plate is no. 1, the primordial plate, the uppermost plate no. 5. a. The first ambulacral plate of the two adjoining ambulacra. b. Buccal plates. × 240.

Fig. 8. Buccal plates of newly metamorphosed *Diadema setosum*; in the centre is seen the first trace of the future mouth. × 240.

Fig. 9. Sucking disk of primordial tubefoot (a) and of the second pair of tubefeet (b) of the young *Diadema setosum*. × 400.

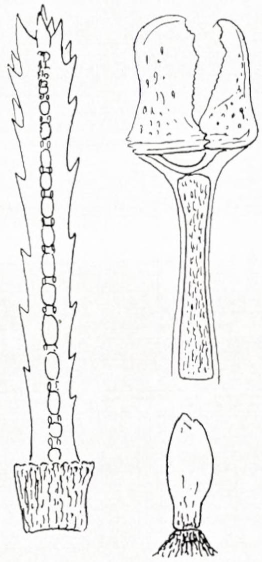
is a complete ring (fig. 9, a); in the following tubefeet to be developed the disk is composed of three separate pieces (fig. 9, b), corresponding to what was found by Gordon in *Psammechinus miliaris* (Op. cit. figs. 12—13).

In the following stage, 2 months of age, the genital plates are fully formed, though the plates 4 and 5 are not yet as large as the others. The original larval rods are still distinguishable. The ocular plates are widely excluded from the periproct, in which no anal plates have as yet been formed (fig. 13). The buccal plates are fully formed, all of equal size; but there are still no buccal tubefeet. The masticatory apparatus is nearly ready, but there is still no mouth or anal opening (fig. 15). In another specimen of the same age there are five anal plates of nearly equal size (fig. 14).



10.

11.



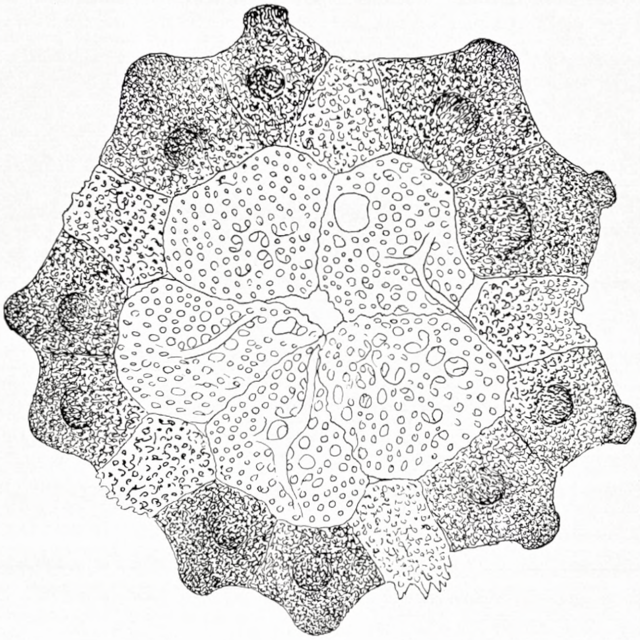
b.

a. c.

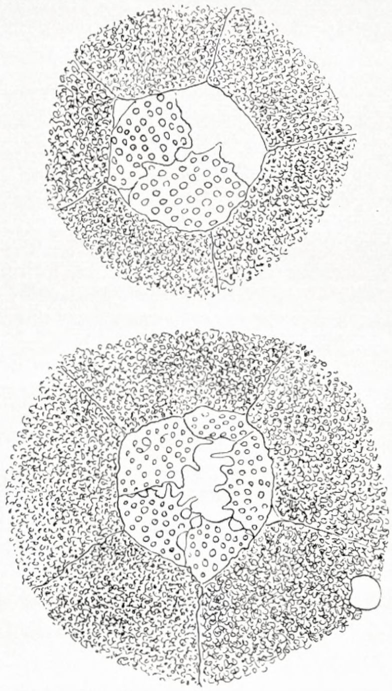
Fig. 12. Spine (a), ophicephalous pedicellaria (b), and sphæridium (c) of young *Diadema setosum*, 8 weeks old. × 250.

Figs. 10—11. Young *Diadema setosum*, 9 weeks old, oral (10) and aboral side (11). g. Gills. × 40.

In one of the oldest specimens, 9 weeks old (figs. 10—11), the buccal feet have been formed. The ocular plates are still widely exsert — a fact of importance, since later on three of them become very broadly insert. In this specimen there are only two anal plates, which shows that no morphological importance attaches to the fact that in the younger specimen there are five anal plates (figs. 14, a-b).



13.



a.

b.

14.

Fig. 13. Denuded test of young *Diadema setosum*, 2 months old. × 150. In three of the genital plates remnants of the larval skeleton are still seen.

Fig. 14. Periproct, with anal plates, and the upper part of the genital plates of young *Diadema setosum*; a. from a specimen 9 weeks old, b. from a specimen 8 weeks old. The large hole in the right lower plate in fig. b. is the primary pore of the madreporite. The same is seen in the right upper genital plate in fig. 13. × 150.

The spines of these young specimens are quite simple, thorny, fenestrated, not of a special embryonal type (fig. 12, a); there are no spines on the apical plates, and as the apical system is relatively large, this looks very naked (fig. 11). Sphæridia have appeared in the specimens of 8 weeks (figs. 12, c; 15). The pedicellariæ are of the ophicephalous type, without neck (fig. 12, b). — The specimens of 8—9 weeks were already black coloured on the aboral side; the rather thick, black skin had to be removed, before the structure of the test could be seen.

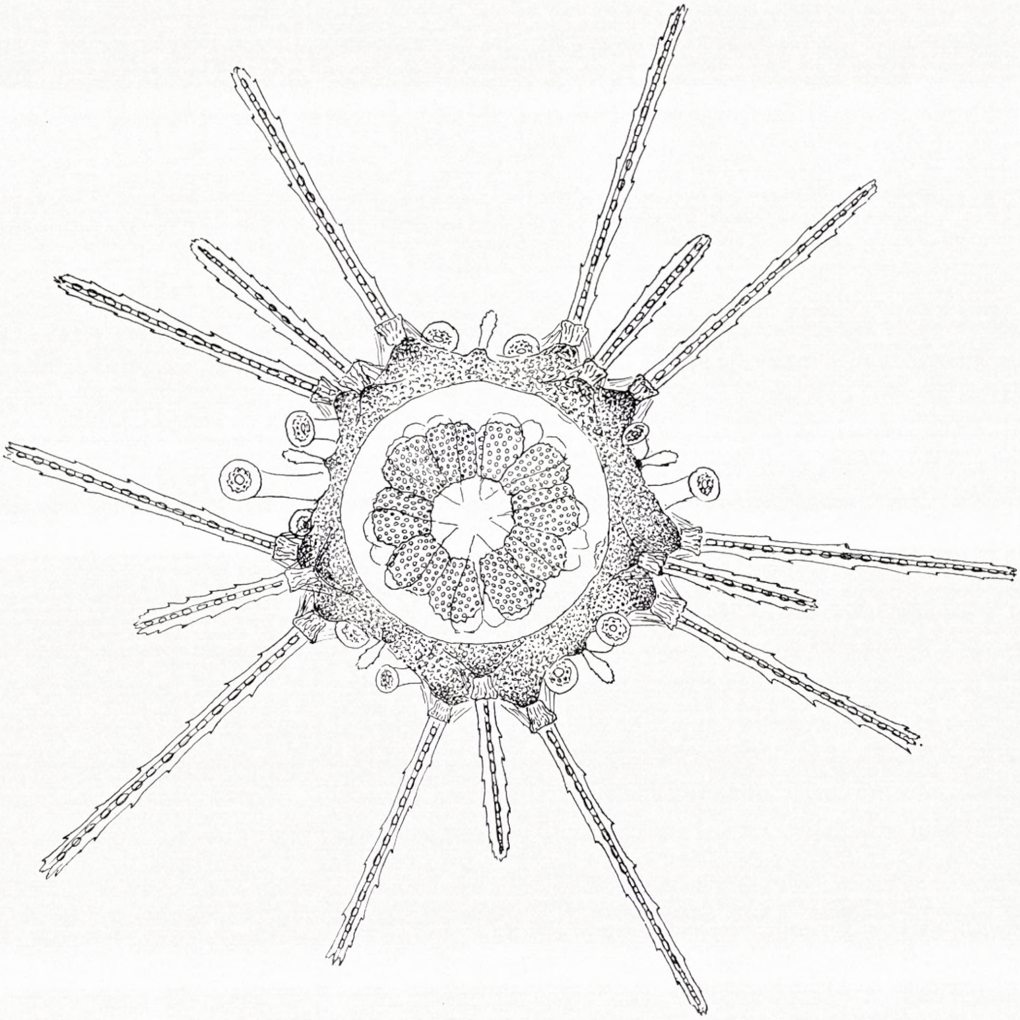


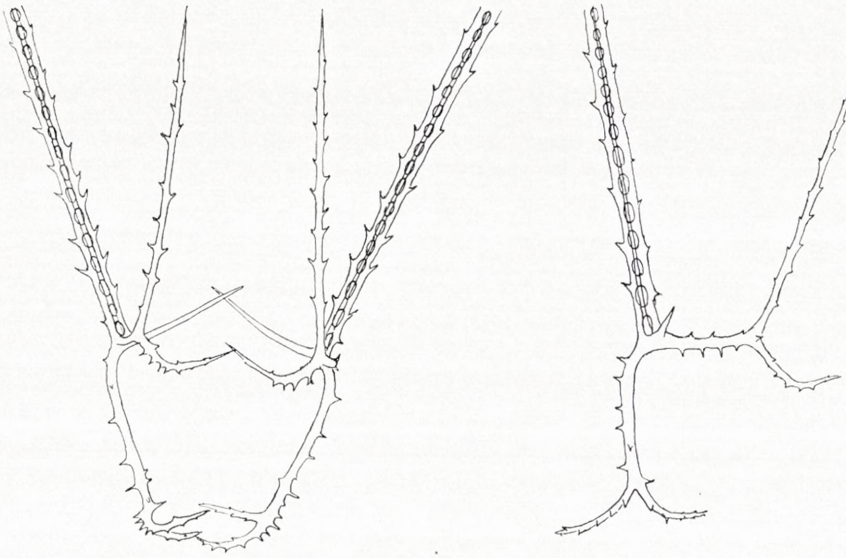
Fig. 15. Young *Diadema setosum*, two months old; oral side. × 90. The masticatory apparatus nearly fully formed, but there is still no mouth-opening; buccal plates fully formed, but the buccal tubefeet have not yet appeared. In the middle of each ambulacrum, between the tubefeet, is seen the first sphæridium.

3. **Temnotrema scillæ** (Mazetti).

Pl. III. Figs. 1—2; Pl. X. Fig. 1.

On the dredging trip to the Gulf of Suez with the "Mabahiss" in the middle of May a good number of specimens of the small Echinoid *Temnotrema scillæ* (Mazetti) were dredged off Ashrafi Light, at a depth of c. 80 meters, on a muddy-sandy bottom. They were taken alive to the laboratory, where I found a few of them to contain some ripe eggs and a little sperma; it was apparently just in the beginning of the breeding season. Fertilization was undertaken on May 15th. The eggs are very small, only c. 0.08 mm., very clear and transparent.

The cleavage passed very rapidly, the 32—64 cell stages being reached already in two hours. There seems to be some inequality in the size of the cleavage cells — but I did not follow the cleavage process in details, so I do not venture to say definitely that there is such inequality. After 22 hours the embryos were gastrulæ, with beginning formation of the skeleton. At the upper end of the archenteron a pair of thin mesoderm-pouches, almost without lumen, proceed, reaching to and apparently attaching themselves to the ectoderm (Pl. X. Fig. 1).



a. b.

Fig. 16. Skeleton of the larva of *Temnotrema scillæ* (Maz.), I. stage. a. From the dorsal side, b. in side view. × 240.

The young pluteus-stage is reached on the second day. It has a typical Temnopleurid skeleton (fig. 16, a-b), with the body rod ending in two diverging branches; there is no basket structure. The postoral rod is fenestrated. The whole skeleton is strongly thorny.

At the age of two weeks the larva had reached its full shape, the first rudiments of the amnion being discernible, and the first pedicellariæ having appeared. This larva (Pl. III. Figs. 1—2) is of great beauty. The four main arms are very broad in the proximal part, but the distal part, about a fourth of the length, is slender, the narrowing being quite abrupt. There is a vibratile epaulet at the base of each of these four arms, but no ventral or dorsal vibratile lobes, whereas the posterolateral lobes are well developed. The anterolateral and preoral arms are quite short and narrow. A number of small reddish pigment spots are scattered all over; they are a little more numerous along the epaulets, but there are none in the end part of the arms. The stomach is a very faint yellowish.

The posterodorsal rod is fenestrated like the postoral ones; the posterior transverse rod is simple, bifurcating at the ends, the lower branch being simple, straight, without thorns (fig. 17). A muscular system makes the four main arms movable.

I did not succeed in rearing the larvæ through metamorphosis, the culture being quite small and only very few larvæ reaching the full shape.

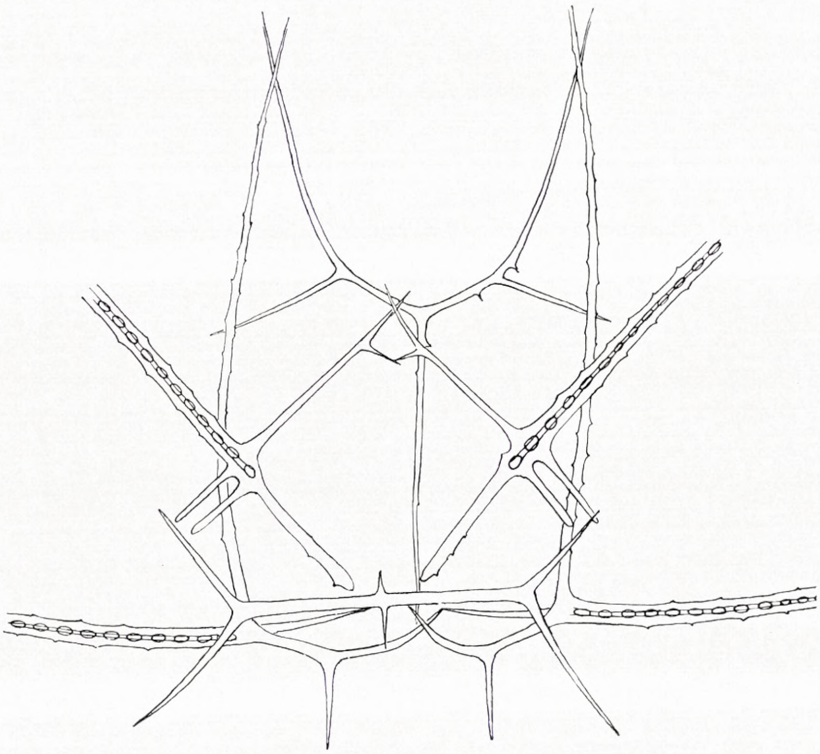


Fig. 17. Skeleton of the fully formed larva of *Temnotrema scillæ* (Maz.). × 250.

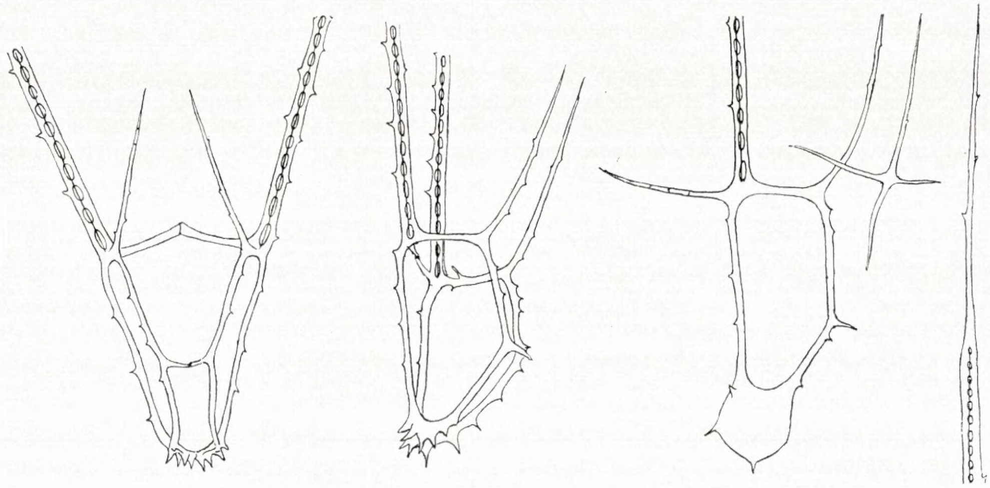
The larva of another species of the genus *Temnotrema*, *T. sculptum* A. Agassiz, was described in my "Studies" of 1921, p. 54, Pl. VI. 4, having been reared during my stay at Misaki, Japan, in April—May 1914. It was, however, not reared till full larval shape, and is thus incompletely known; but so far as known, it agrees in the main features with the larva of *Temnotrema scillæ*.

4. **Nudechinus Gravieri** (Koehler).

Pl. IV. Fig. 1.

This little Echinoid, which occurs fairly commonly under stones on the reef flat at the coast, as well as on sandy bottom at a depth of c. 5—10 m off the Abu Sadaf reef at Ghardaqa, was found ripe early in May, and fertilization was undertaken on May 7th. The eggs are c. 0.09 mm., very clear and transparent. Development proceeds rapidly, the embryos having begun to assume the Pluteus-shape already after about 20 hours.

In the young larva, stage I, the body skeleton forms a typical basket structure, the posterior end of the body rods being rather broad and strongly thorny (fig. 18, a, b); the postoral rod is fenestrated. Very soon, by the time the posterodorsal rod appears, a remarkable thickening of the posterior part of the basket sets in (figs. 18, c; 19, a). By the time the dorsal arch appears, the recurrent rod begins to be resorbed (fig. 19, b), and when the posterior transverse rod appears, scarcely a trace of the recurrent rod



a. b. c. d.

Fig. 18. Skeleton of the larva, I. stage, of *Nudechinus Gravieri* (Koehler); a. from the aboral side. b. in side view. c. Skeleton of a slightly older larva, side view, showing the thickening of the posterior end of the basket; the posterodorsal rod has appeared. d. Terminal part of postoral rod. × 240.

is left, and the large terminal swelling is borne alone by the body rod, which now looks exactly like a golf club (figs. 19, b, c). With the growth of the transverse rod, the terminal swellings begin to dissolve; they no longer join in the midline, and then the body rod breaks, and the two balls remain lying in the posterior end of the body, one to each side of the first pedicellaria, gradually becoming smaller, evidently resorbed and their calcareous matter used in the formation of the skeleton of the young sea-urchin (fig. 19, d). The posterodorsal rods are simple, and the fenestrated postoral rods terminate as a simple rod (fig. 18, d). The ventral transverse rods are unusually long. The posterior transverse rod is of a quite unusual shape, like a bow, the upturned ends not bifurcating (fig. 19, d).

The fully formed larva (Pl. IV. Fig. 1) has rather short arms, the four main arms being wide in the basal part, slender in the distal part. There is a pair of large vibratile lobes on the ventral side, the corresponding dorsal lobes being smaller.

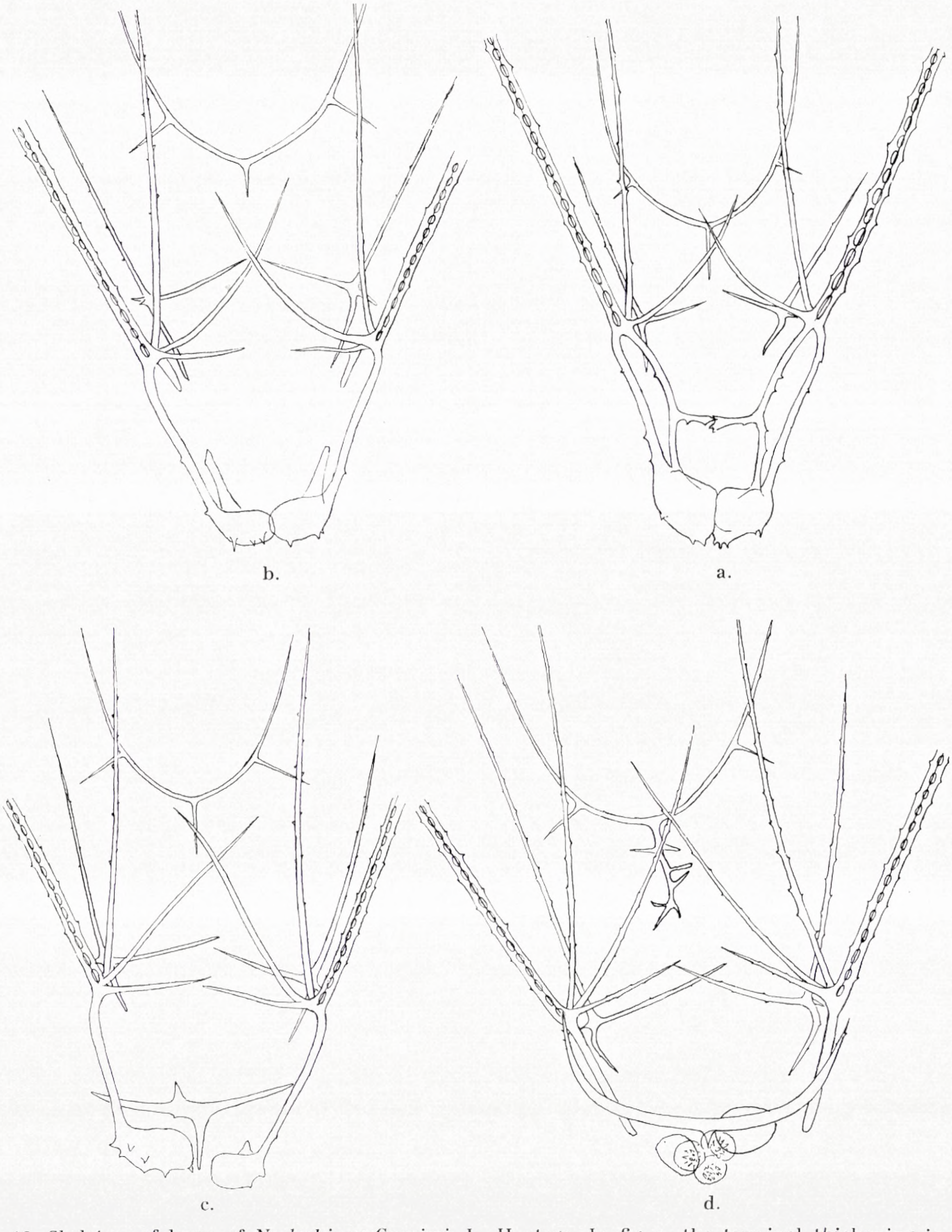


Fig. 19. Skeleton of larva of *Nudechinus Gravieri*, I—II. stage. In fig. a. the terminal thickening is seen fully developed; in fig. b. the recurrent rod has begun to be resorbed; in fig. c. only the last vestige of it is seen on the right side; the posterior transverse rod has appeared. In fig. d. the last rests of the thickening are seen in the middle of the posterior end, beside the incipient first pedicellaria. The posterior transverse rod is fully formed. × 240.

Below the lobes are a pair of large epaulets, which originate from the outer corners of the vibratile lobes, gradually growing inwards and finally meeting in the midline so as to form a broad transverse band across the ventral and dorsal side of the body. The posterolateral lobes are small. The colour is very marked on account of a large dark brownish patch on the middle of each arm, in the large ventral lobes, and in the produced corners of the postoral area. Besides, there are some scattered small reddish spots, more numerous along the epaulets, which also have a light tinge of yellowish.

A couple of the larvæ metamorphosed, but as, unfortunately, the skeleton of the preserved specimens had been completely dissolved (on account of acid from the cork?), I cannot give any information of the skeletal structure.

This very interesting larva agrees in the main with the Toxopneustid larval type, but shows such surprising special features as were hardly to be expected in a genus, the main distinctive character of which is the complete absence of deposits in the buccal membrane (excepting, of course, the buccal plates), a character that would not beforehand seem to be of great morphological importance. But evidently then it is a very important character.

It seems beyond doubt that the larva described in my "Studies" 1921, p. 60, Pl. XI. 3, as Echinopluteus of Temnopleurid (?) species c. must be very closely related to the *Nudechinus* larva, as it agrees with the latter in the main characters of the skeleton — the peculiar shape of the posterior transverse rod, the postoral rods terminating in a simple point, the posterodorsal rods simple. It is then certainly not a Temnopleurid larva. No *Nudechinus* species being known from off Jolo, where this larva was found, the suggestion lies at hand that it is the larva of a *Gymnechinus*, but this can be no more than a suggestion at present. The fact that there is no terminal swelling of the body rods (I have reexamined the specimens for ascertaining this point) does indicate that it belongs to another genus.

5. **Tripneustes gratilla** (Linn.).

Pl. IV. Fig. 2.

The development of this species has been dealt with repeatedly. In my "Studies" 1921, p. 34, Pl. VIII. 5—6 I described the young larva, reared during a stay at Hilo, Hawaii, in March—April 1915. In my "Contributions" I—II, 1931, p. 24, Pl. III. 5, I gave a more detailed description of the first development stages, and a coloured figure of the larva by the end of the first stage, reared at Mauritius in September 1929; but although the larvæ lived for more than five weeks they did not reach the final shape. — Further, Onoda, in his paper of 1936, p. 647, Pl. XIII. 8—9, again figures the larva in the I. stage (and an embryo showing the beginning formation of the skeleton). It may suffice then here to describe and figure the as yet unknown fully formed larva. Fertilization was undertaken at Ghardaqa the 29th of April, and at the age of about 18 days several of the larvæ were in beginning metamorphosis.

This proves that the long time it took for the larvæ at Mauritius to begin only to pass into the second larval stage, c. 30 days, was due to unfavourable circumstances, as I suggested (Op. cit.).

The fully formed larva (Pl. IV. Fig. 2) is a very beautiful object, with large vibratile lobes on the ventral and dorsal sides and at the posterior corners. The corners of the postoral area are produced into narrow lobes.

The diagrammatic figure 20 shows the arrangement of the vibratile lobes. The postoral and posterodorsal arms are rather broad, not very long (— the posterodorsal arms gradually reach the same length as the postoral ones —); the anterolateral and preoral arms are quite short, but the frontal lobe is high. The colour consists of

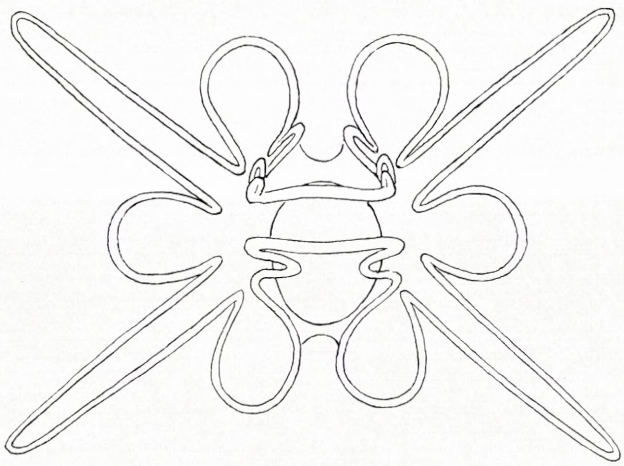


Fig. 29. Diagrammatic figure of the fully formed larva of *Tripneustes gratilla* (L.), showing the relation of the vibratile lobes to the four main arms.

scattered irregular carmine spots, somewhat more prominent along the vibratile band of the lobes. The postoral rod is fenestrated, but the terminal part is simple; the posterodorsal rods are simple, unfenestrated. The posterior transverse rod is simple, straight, with a bifurcation at the ends, the lower branch being simple, straight, a little longer than the upper one.

The young postembryonal stages were not observed.

As was to be expected the larva of *Tripneustes gratilla* is like that of *Tr. esculentus* (cf. "Studies", 1921, Pl. II) in all main features, so much so, indeed, that I doubt whether it would be possible to distinguish them with certainty from one another, if specimens of both were mixed together.

6. **Echinometra Mathæi** (Blv.).

Pl. V. Fig. 1.

As was the case with *Tripneustes gratilla*, the development of this species has been the object of repeated studies. The first note on its development was given in my "Studies" 1921, p. 75, from my stay at Hilo, Hawaii, in April 1915. Next TENNENT (Early development and larval forms of three Echinoids of the Torres Strait region. Publ. Carnegie Inst. No. 391, 1929, p. 118) gave a detailed description and figures of the earliest stages till the I. larval stage. Finally ONODA in his paper of 1936, p. 641, Pls. XI. 5—7; XII. 1—2, described and figured the larva from the young, beginning pluteus to the fully formed larva in beginning metamorphosis. I can thus confine myself here to giving a coloured figure of the fully formed larva (Pl. V. Fig. 1).

Comparison of this figure with ONODA's Pl. XII. Fig. 2 shows a rather conspicuous difference between them. As regards the postoral region and the ventral and dorsal vibratile lobes, the difference may be due to the different mode of drawing, and a different stage of contraction in these parts, when they were drawn (my figure represents them in a state of non-contraction); but as for the posterolateral lobes I have never seen the vibratile band to develop into such conspicuous epaulets as shown in ONODA's figure, even in stages as far advanced as that shown in ONODA's figure.

The colour of the larva consists of scattered small carmine spots, somewhat more numerous in the ends of the main arms and along the band of the vibratile lobes.

This larva was reared at Ghardaqa in April—May, the full larval form being reached in about 18 days, whereas ONODA found the metamorphosis to begin only after 40 days. This fact again shows the great variation in the time required for the development, depending, evidently, on the conditions of temperature, food, etc.

As was to be expected, this larva resembles that of *Echinometra lucunter* ("Studies" 1921, Pl. I) very closely, there being only very minor points of difference, if, indeed, any.

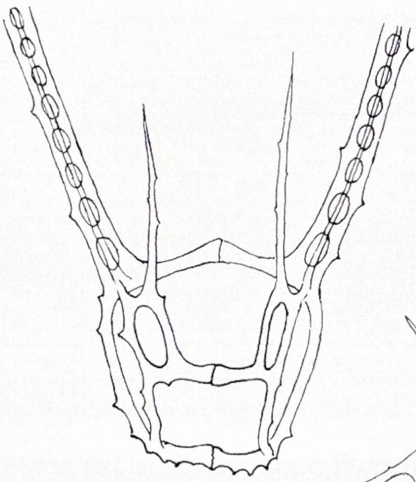
7. **Heterocentrotus mammillatus** (Linn.).

Pl. V. Fig. 2.

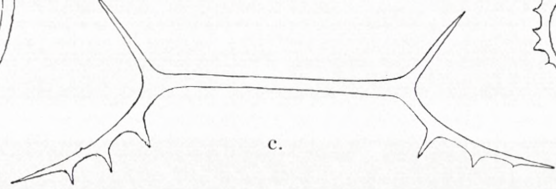
Till now our knowledge of the development of *Heterocentrotus mammillatus* was confined to the observations recorded in my "Studies" 1921, p. 77, amounting to little more than that it has a pelagic larva, probably of the Echinometrid type. It was therefore a matter of satisfaction that this species, which is fairly common on the reefs of Ghardaqa, proved to be ripe already in April, so that fertilization could be undertaken one of the first days of my stay at the station, April 23rd. The culture was fairly good, the larvæ not very numerous, but I succeeded in rearing them to full larval shape, and a few of them even through metamorphosis.

The eggs are of the usual small size, c. 0.1 mm, not very clear. The early development processes did not offer anything of special interest. The skeleton begins to develop at the age of 24 hours, and at the age of two days the embryos have assumed the Pluteus-shape, beautifully coloured with scattered small red spots. The skeleton is that typical of the Echinometrid larvæ, the body skeleton forming a complicate basket structure, the recurrent rod being double (figs. 21, a, b); it is rather strongly thorny. The postoral rod is fenestrated.

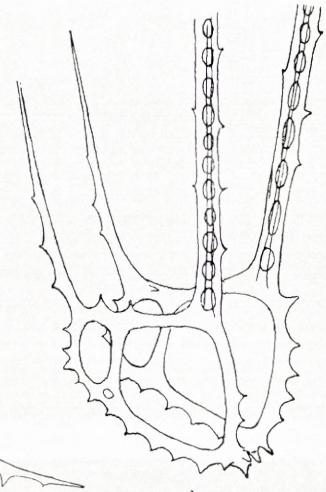
The full larval shape was reached after about three weeks. The larva has rather unusually long and slender arms, not only the four main arms but also the anterolateral



a.



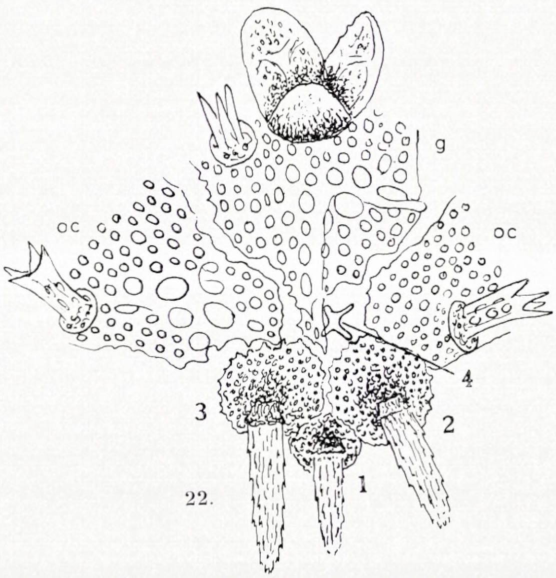
c.



b.

Fig. 21. Skeleton of the larva of *Heterocentrotus mammillatus*, I. stage, from the aboral side (a) and in side view (b). Posterior transverse rod of fully formed larva (c). × 300.

and preoral ones (Pl. V. Fig. 2). There are well developed ventral, dorsal[1], and posterolateral lobes, and also the corners of the postoral area are produced so as



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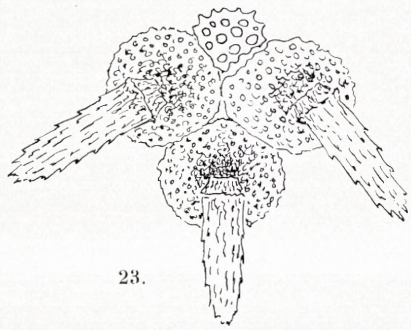


23.

Fig. 22. An interambulacrum, with part of the adjoining apical plates of young *Heterocentrotus mammillatus*. Interambulacral plate no. 4 has just begun to develop. g. Genital plate (with pedicellaria); oc. ocular plates. Embryonal spines have appeared on the apical plates. × 300.

Fig. 23. Interambulacrum of slightly older specimen. Plate no. 4 is seen lying in the midline. × 300.

to form narrow lobes. The colour consists of isolated red spots, more numerous along the band of the vibratile lobes, the postoral and preoral band, and in the point of the arms.

[1] The dorsal lobes are not shown in Pl. V. Fig. 2; but they are as well developed as the ventral ones.

The posterior transverse rod (fig. 21, c) is of the usual Echinometrid type, the lower branch of the terminal bifurcation with some thorns along its underside. Both postoral and posterodorsal rods fenestrated in their whole length; the anterolateral and preoral rods rather strongly thorny.

On the 3rd of June I found a couple of specimens metamorphosed. They show the genital plates developing around the basal parts of the larval skeleton, in the usual

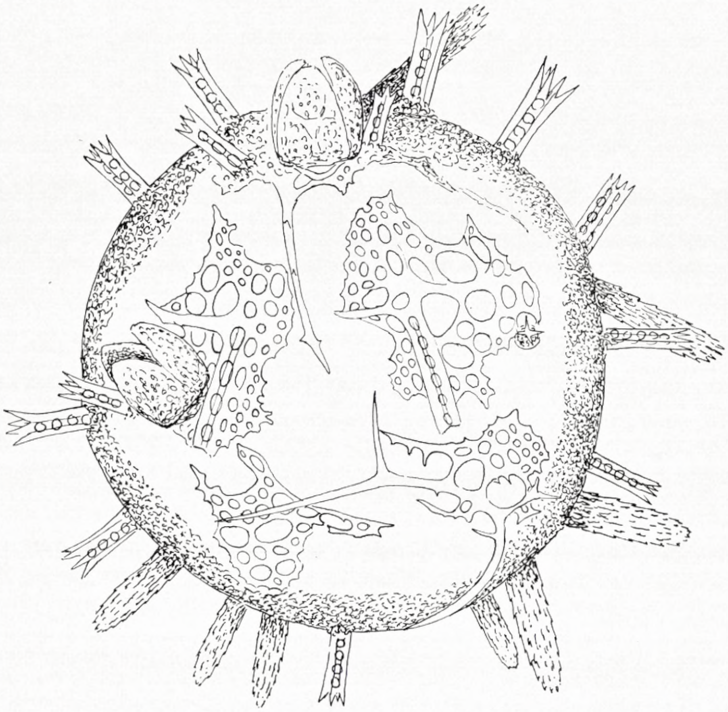


Fig. 24. Young *Heterocentrotus mammillatus*, just metamorphosed, 6 weeks old. From the aboral side × 225.

way (fig. 24). The buccal plates are only partly developed (fig. 25), one preceding the other in each pair, in one radius only one of the buccal plates has appeared. The first rudiments of the masticatory apparatus are seen in three of the radii; the first pair of ambulacral plates have appeared in three of the radii, but not in the two others. The mouth opening not yet formed. Only the primary tubefoot has developed. In the interambulacra only the four first plates are formed (figs. 22—23), plate 4 lying in the middline as known from *Psammechinus miliaris* (cf. Gordon, Op. cit.). The spines of the apical plates end in four points, being of an embryonal type. The spines of the interambulacral plates are already rather thick, as might be expected in view of the character of the spines of the adult. — No specimen developed beyond this stage.

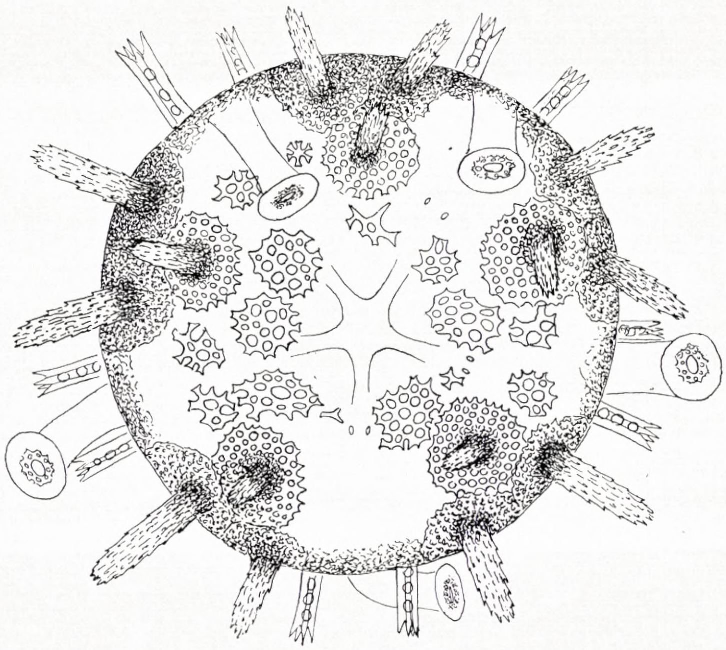
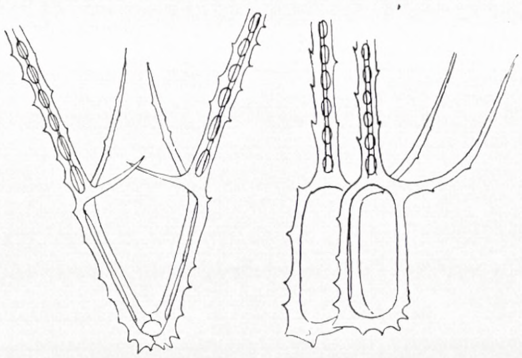


Fig. 25. Young *Heterocentrotus mammillatus,* just metamorphosed, 6 weeks old. From the oral side × 225.

8. **Fibularia craniolaris** (Leske).

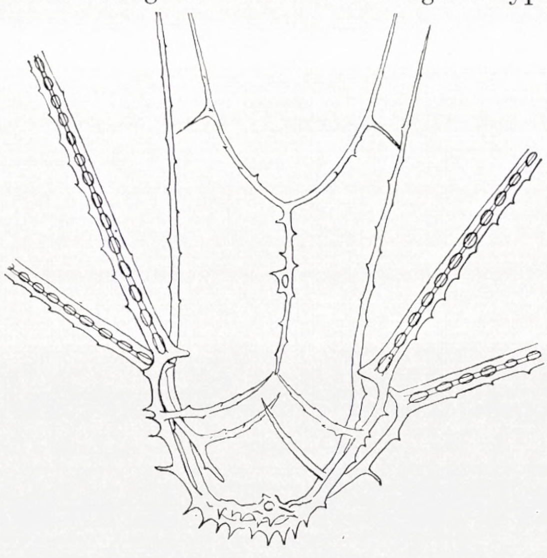
Pl. VII. Fig. 1.

Fertilization of this species, which occurs in fair numbers on sandy bottom at a depth of c. 5—10 m. off Ghardaqa, was undertaken on May the 7th. The eggs are very small, c. 0.09 mm., very clear. The cleavage is of the usual regular type.



a. 26. b.

Fig. 26. Skeleton of larva of *Fibularia craniolaris*, I. stage, from the oral side (a) and in side view (b). In fig. b. the two halves of the skeleton have been slightly displaced. × 250.



27.

Fig. 27. Skeleton of fully formed larva of *Fibularia craniolaris*. × 250.

On the second day the embryos were beautiful plutei of the I. stage. The body skeleton (figs. 26, a, b) forms a basket structure, rather thorny; the postoral rods are fenestrated.

The fully formed larva (Pl. VII. Fig. 1), two weeks old, is a very active swimmer, standing usually in a vertical position directly under the surface. It is of quite simple shape, without vibratile lobes; only between the two main arms there is a small prominence, outlined by the vibratile band. The colour is very feeble, only a faint yellowish-brown in the ends of the four main arms. In the skeleton the curious feature is observed that the original ventral transverse rod has almost disappeared and a new one developed some distance below on the body rod. The posterior part of the body skeleton has become a little more thorny and more complicate, forming an irregular, fenestrated plate of varying size. The posterodorsal rod is fenestrated like the postoral rod (fig. 27).

Some of the larvæ metamorphosed; but I missed the metamorphosis-stages, the youngest stage preserved being already a fully formed sea-urchin, so I cannot give information about the postembryonal development of this species, which will, no doubt, be quite conform with that of *Echinocyamus*, so fully described by THÉEL in his excellent paper "On the development of *Echinocyamus pusillus*" (Nova Acta R. Soc. Sc. Upsala. III. 1892). Also the larva is very similar to that of *Echinocyamus pusillus* (cf. my "Contributions" 1931. Pl. IV. 2), as might be expected on account of the undoubtedly close relation between the genera *Fibularia* and *Echinocyamus.*

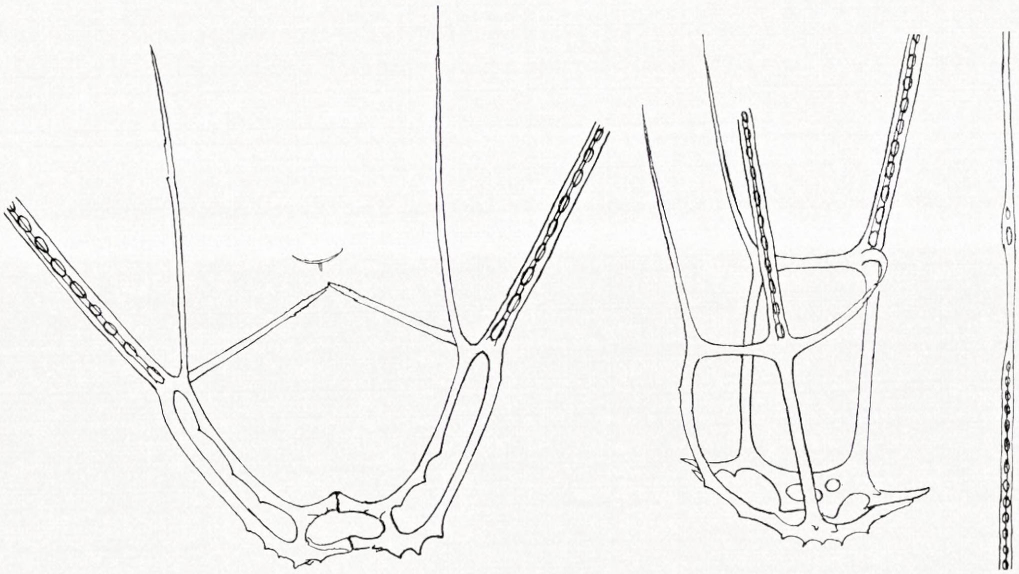
9. **Clypeaster humilis** (Leske).

Pl. VI. Figs. 1—2.

Specimens of this species examined on April the 22nd were found to be in the end of spawning, but there was still enough of eggs and sperma for making a fertilization, which proved very successful. The eggs are of the usual small size, c. 0.1 mm., very clear and transparent. The fertilization membrane stands widely out from the surface of the egg; I did not notice any mucilaginous coat around the eggs, such as I found to exist in *Clypeaster japonicus* ("Studies" 1921, p. 95). The cleavage is regular. At the age of one day the gastrula is beginning to form, at the age of three days the first Pluteus-stage is reached. The postoral arms gradually become quite broad and flat and have a conspicuous carmine spot at the end; also a few small spots of the same colour are found scattered on the body. The body skeleton is a typical basket (fig. 28, a, b), very smooth, only the posterior connecting rod is a little thorny, may even be a little widened, fenestrated. The ventral transverse rods are finely thorny towards the end. The postoral rod is finely fenestrated, perfectly smooth.

The fully formed larva, about two weeks old, is a strikingly beautiful object (Pl. VI. Figs. 1—2). The arms are very broad, moderately long, the anterolateral and preoral arms quite short; there are large vibratile lobes, ventral, dorsal, and posterolateral, and further the corners of the postoral area are produced so as to form small lobes, and on the middle of the dorsal side the vibratile band forms a large, slightly raised fold. In the end of each arm (except the preoral ones) and likewise in all the lobes there is a conspicuous carmine spot; red spots are found sparsely all along the vibratile band, and some scattered small red spots in the posterior end of the body.

The skeleton of the fully formed larva affords unusually interesting features. The body skeleton gradually becomes completely resorbed, the four main rods terminating as quite simple rods in the body; also the ventral transverse rods disappear. But a more extraordinary fact is that the postoral rods, which originally are fenestrated



a. b. c.

Fig. 28. Skeleton of larva of *Clypeaster humilis*, I. stage, seen from the dorsal side (a) and in side view (b). Part of postoral rod transforming from the original fenestrated condition into a simple rod (c). × 300.

throughout, gradually transform into simple, exceedingly slender rods, the transformation beginning at the point of the rod about at the time when the posterodorsal rods and the dorsal arch appear. Not only the holes of the rod disappear, but the whole rod becomes thinner than in the I stage (fig. 28, c); thus a very remarkable resorption and reapposition of the calcareous matter must take place. The posterodorsal rod is simple from the beginning. On the whole the skeleton is very delicate.

Some of the larvæ metamorphosed, but not having preserved any of the metamorphosis-stages, I cannot give any information about the development of the skeleton of the young sea-urchin.

The only other *Clypeaster*-species the development of which has been studied is *Clypeaster japonicus* Döderl.; only the first larval stage of this species is known (cf. my "Studies" 1921, p. 95, Pl. XIV. 3), but judging therefrom the fully formed larva may be expected to be similar to that of *Clypeaster humilis*. This seems to indicate that there is a special type of larva in the family of the Clypeastridæ, differing from that of the other Clypeastroids in the large vibratile lobes, the resorption of the body skeleton, and the transformation of the postoral rods from originally fenestrated into simple rods.

10. **Echinodiscus auritus** Leske.

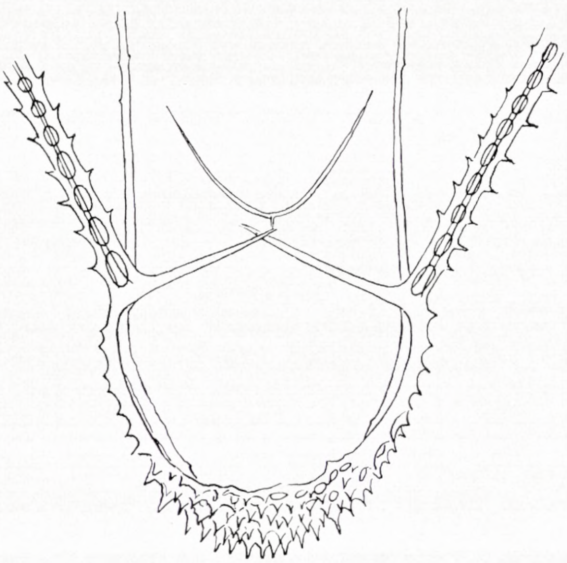
Pl. VII. Fig. 2.

In the immediate neighbourhood of Ghardaqa this species does not occur, so far as known; but the sailors brought home some specimens from Abu Mingar on June the 1st. They proved to contain ripe sexual products, and fertilization was undertaken. The eggs are surrounded by a thick mucilaginous coat with purple spots, such as I have found to exist in several other Clypeastrids (cf. "Studies" 1921, p. 107, fig. 43). The spermatozoa penetrate through this coat, as I was able to ascertain here. It is uncertain, whether the coat is found on the normally spawned eggs; at least it disappears almost immediately after the fertilization membrane has been formed (inside the coat). The eggs are not very clear, and the embryos correspondingly rather opaque. After 30 hours the embryos were small plutei, and in the two days old larvæ the posterodorsal rods and the dorsal arch have already begun to form. At the age of five days the larvæ had reached their full size (Pl. VII. Fig. 2); the four main arms could now be moved actively, the body skeleton having thus already been partly resorbed.

By this very fast development from the egg to full larval shape I very naturally expected to see them metamorphose very soon — but herein I was strongly disappointed. Although the cultures seemed to be in good condition, the larvæ living apparently quite well for a long time, only a couple of the larvæ showed the first sign of metamorphosis (the amnion), and by the end of June the larvæ began to deteriorate.

The fully formed larva (Pl. VII. Fig. 2) is very much like the *Mellita* and *Astriclypeus* larvæ figured in my "Studies" 1921, Pl. IV, being without vibratile lobes, in striking contradistinction to the *Clypeaster* larva. It has a patch of red colour in the end of the postoral arms, and some scattered small red spots particularly in the quite intransparent hind end of the body. Along the vibratile band and over the stomach there are a number of small, oval, yellow spots. On the whole the colour is rather faint.

The skeleton of the young larva is very characteristic, the posterior part of the body skeleton forming a large, irregular, fenestrated, and strongly thorny plate (figs. 29—30). The postoral and posterodorsal rods are fenestrated, strongly thorny till the point. In the fully formed larva the body rod is partly dissolved, the fenestrated plate in the posterior end of the body remaining connected only with the recurrent and the anterolateral rod; also the connection between the postoral rod and the recurrent and anterolateral rods is severed; the postoral arms thus become movable like the posterodorsal arms, the skeletal rod of the latter having never been coalesced with



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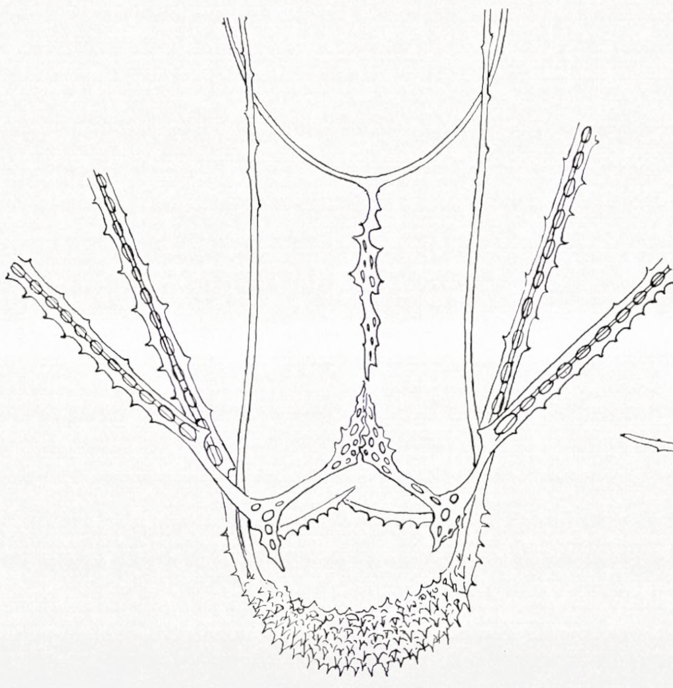

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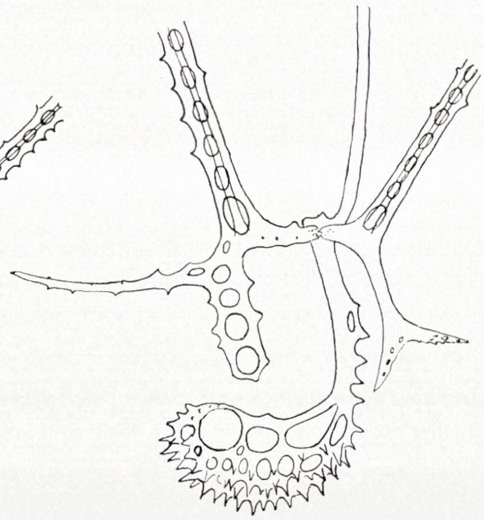


32.

Figs. 29—32. Skeleton of the *Echinodiscus auritus* larva; 29—30. of the young larva, from the oral side (29) and in side view (30). Fig. 31. shows the skeleton of the fully formed larva, from the dorsal side; fig. 32. shows the beginning resorption of the body rod, side view. × 300.

the body skeleton (figs. 31—32). Whether the large plate in the posterior end of the body is resorbed or enters into the final skeleton remains an unsolved question for the present.

11. **Lovenia elongata** (Gray).

Pl. VII. Fig. 3.

Some specimens of this fine species were dredged on sandy bottom at a depth of c. 10—20 meters off the Abu Sadaf reef, close to the station, as also some specimens were found living in the sand in quite shallow water close to the station (together with *Astropecten polyacanthus* and *Luidia Savignyi*).

Fertilization was undertaken on May the 4th. The eggs are of the usual small size, c. 0.09 mm., very clear and transparent. The cleavage passes very rapidly, the embryos being swimming blastulæ already after 6—7 hours, "beautiful as a diagram" I have said in my notebook. At the age of 18 hours they were small plutei, strongly

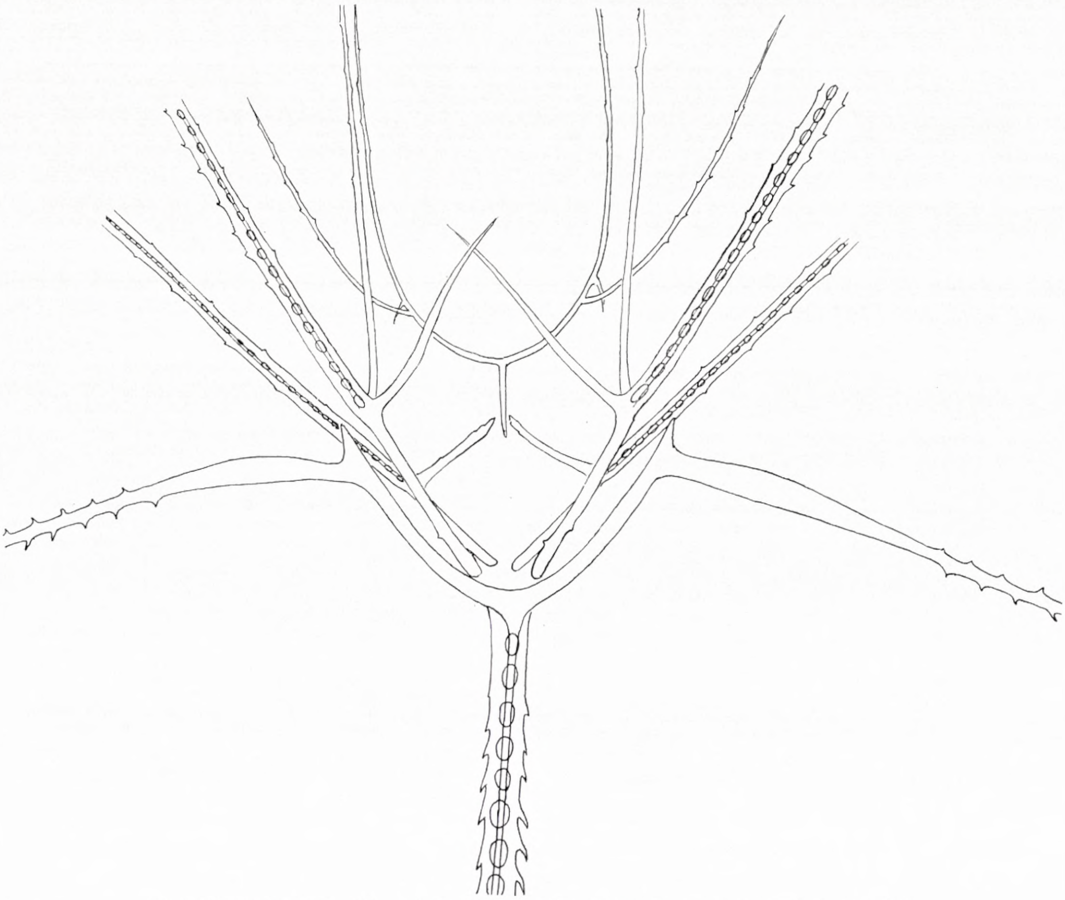


Fig. 33. Skeleton of the fully formed larva of *Lovenia elongata*. × 240.

pigmented, particularly a carmine patch in the end of the postoral arms and in the posterior end of the body; at the age of 25 hours the posterior rod had begun to form. At the age of 12 days the full larval shape (Pl. VII. Fig. 3) is reached, the posterolateral arms having developed, and the amnion appeared. It is a perfectly typical Spatangoid larva, with a very long posterior process, with a large carmine spot in the end. Also the postoral, posterodorsal, and posterolateral arms have a conspicuous carmine spot in the end; scattered small spots of the same colour are found in the body and arms, and a larger spot below the postoral and above the preoral band. The stomach is a light yellow.

The skeleton (fig. 33) is quite the usual type, the only special feature being a light swelling of the basal part of the posterolateral rods. Both postoral and posterodorsal rods are fenestrated and thorny throughout, the holes in the posterodorsal rod being distinctly smaller than those of the postoral rod.

The larva of this species — no *Lovenia* larva being known till now — serves to emphasise the uniformity of the larvæ within the family of the Spatangidæ.

Asteroidea.

12. **Astropecten polyacanthus** Müller & Troschel.

Pl. X. Figs. 2, 5.

This species, which lives in good numbers in the sand in shallow water at the station, was found to have ripe sexual products by the end of May. I was greatly surprised in finding this species to have serial gonads, other *Astropecten* species having only a single, large gonad on each side at the base of the arm. This raises the question, whether all the forms usually identified as *Astropecten polyacanthus* are really the same as the Red Sea form, which latter is the typical *polyacanthus*, Müller & Troschel having based their description of *A. polyacanthus* on specimens from the Red Sea. Particularly it seems that the Japanese form, originally described by Müller & Troschel as *Astropecten armatus*, cannot really be identical with the true *polyacanthus*, as is otherwise generally accepted. I have reared the larva of this Japanese form ("Studies" 1921, p. 186) after artificial fertilization. It is rather unthinkable that I should not have noticed it, if it had serial gonads; but I have said nothing about it. And on opening a specimen preserved in alcohol I also find it to have only one gonad on each side at the base of the arm (— so far as it is possible to make sure on an old specimen, in which the gonads are very hard and brittle —). But it is quite out of question that specimens of so different anatomical characters, some having serial gonads, others single gonads, could belong to one and the same species — it would rather seem questionable whether they can really be referred to the same genus. — It is not the place here to enter into details of this question; but after this discovery of the true *A. polyacanthus* having serial gonads it will be necessary to investigate the anatomy of also the other *Astropecten* species and eventually subdivide the large genus *Astropecten* after the character of the gonads.

Fertilization of *A. polyacanthus* was undertaken on May the 26th; it proved successful, and I had a good number of gastrulæ the next day. The fertilization being made late in the afternoon I had no opportunity of ascertaining whether the blastulæ are folded within the egg-membrane as is so often the case in Asteroids. The development proceeds very rapidly, the larvæ having reached their full shape and beginning to metamorphose already on the third day. The larva (Pl. X. Figs. 2, 5) is of the simple type, without Brachiolaria-stage; it is nearly colourless, only with the merest indication of a yellowish tinge on the vibratile bands and the stomach. Numerous small glandular cells are found along the vibratile band and also scattered over the body.

Several of the larvæ metamorphosed; the young sea-stars do not offer any features of special interest, so I think it superfluous to figure them.

13. **Astropecten velitaris** v. Martens.

Pl. X. Fig. 3.

On muddy bottom outside the station, at a depth of c. 10—20 m., this beautiful little species is quite common. It was found to be ripe at the end of May, and fertilization was undertaken on May the 27th. This species has single gonads. It was very difficult to induce the spermatozoa to move, even by adding NaOH (— which had also to be used by *A. polyacanthus* —), and only very few eggs were fertilized. In all I got only c. 50 normal gastrulæ, but as they were rather large it was easy enough to deal with them, and they developed quite normally, though not quite as fast as *A. polyacanthus*, the metamorphosis not beginning till the 5th day. The larvæ of this species, as well as of *A. polyacanthus*, are very active swimmers, usually keeping close to the surface, swimming horizontally.

The fully formed larva (Pl. X. Fig. 3) is so closely alike that of *polyacanthus* that I do not think it possible to distinguish them with certainty; I have, however, not observed the glandular cells along the vibratile band in this species, so this may perhaps prove to be a specific difference.

The larvæ metamorphosed, the young sea-star being indistinguishable from the young *polyacanthus*.

As we know now with certainty the larvæ of five different species of *Astropecten*, *A. irregularis*, *aranciacus*, *scoparius*, *polyacanthus*, and *velitaris*, all these larvæ being so closely alike as to be hardly distinguishable from one another, we can now say with certainty that there is a special type of Bipinnaria corresponding to the family Astropectinidæ, characterized by its broad, round anterior lobes and by having no Brachiolaria stage. The larval body is completely absorbed during the metamorphosis.

14. **Asterope carinifera** (Lamarck).

Pl. X. Fig. 4.

Two specimens of this species — the only ones seen — were brought by the sailors on April the 24th from the outer reef. They proved to be a male and a female, both ripe, and fertilization was undertaken and proved to be successful. The eggs are rather large, c. 0.2 mm., reddish. The fertilization membrane is very clear, widely outstanding. The embryo is folded within the membrane. The gastrula stage was reached on the next day; the gastrulæ are rather elongate. At the age of three days the larval mouth had been formed, but as yet no vibratile band differentiated, the first indication of the preoral band appearing on the fourth day. At the age of six days the band is complete. The development on the whole proceeds slowly, particularly as compared with the *Astropecten* larvæ, the full larval shape and beginning metamorphosis not being reached until at the age of one month. The larvæ are strong swimmers, keeping close under the surface of the water, swimming horizontally.

The fully formed larva (Pl. X. Fig. 4) is a Brachiolaria, having a sucking disk and Brachiolaria-arms, without papillæ, however, — possibly such will appear later on, when the larva is about to metamorphose. The larva is characteristic by the dorsal median lobe being much shorter than the ventral, and by the dorsal side being conspicuously broader than the ventral side. The posterolateral arms are short, not contractile. The colour is a very faint yellowish, which is scarcely stronger on the vibratile band; only the stomach is more distinctly yellowish-grey. There are a number of gland-cells in the vibratile band, particularly that of the anterior lobe. The fact that the preoral band is strongly upwards bent in the young larva figured in my "Studies" Pl. XXXIII. 6 is evidently due to contraction on preservation.

None of the — very few — larvæ metamorphosed.

The young larva of this species I described in my "Studies" 1921, Pl. XXXIII. 6, having reared it at Hilo, Hawaii, in April 1915, when I likewise found its development to pass very slowly, the larvæ having not yet reached their full shape when 26 days old. It is very satisfactory now to have ascertained that this larva has a Brachiolaria stage, as was to be expected from the fact that the related *Porania* larva has such a stage (cf. Gemmill. The larva of the starfish Porania pulvillus (O. F. M.). Qu. J. Micr. Sc. 61. 1915. Pl. 5). In general these two larvæ are much alike, apart from the existence of series of papillæ along the Brachiolaria-arms and the anterior lobe in the *Porania* larva.

Ophiuroidea.

15. **Ophiothrix triloba** v. Martens.[1]

Pl. IX. Figs. 2—3.

Some specimens of this species, which is not rare in the coral blocks on the reefs at Ghardaqa, spawned during the night of May 21st, being kept in a rather small dish. The eggs are red, apparently rich in yolk, and I rather expected that they would not develop into a typical Ophiopluteus, which they did, however. Two days old the embryos were already young plutei, distinctly of the *Ophiothrix* type.

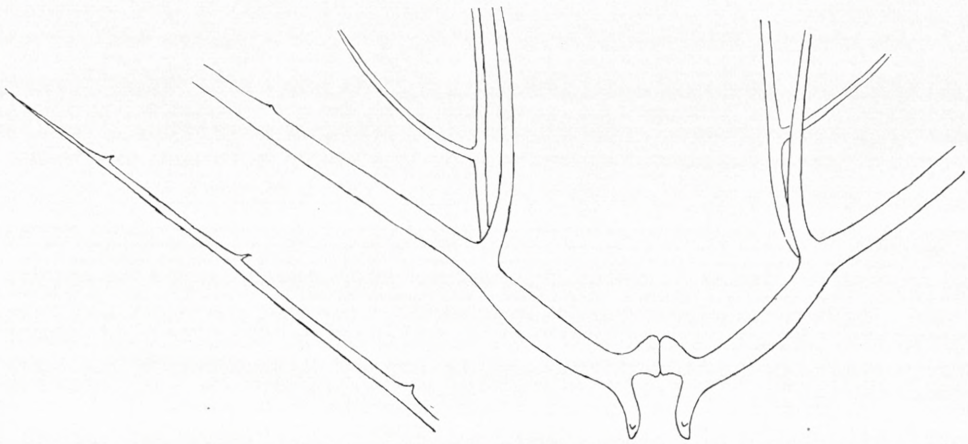


Fig. 34. a. Skeleton of the larva of *Ophiothrix triloba* v. Martens; b. end of the posterolateral rod. × 250.

The young embryos, 12 hours old, did not show the "crest" of vacuolated cells described by MacBride in his paper on "The development of Ophiothrix fragilis" (Qu. J. Micr. Sc. 51. 1907. Pl. 31. 3—5; 33. 25—28); they were simply round, red internally. This red colour is seen again in the stomach of the young larva (Pl. IX. Fig. 2), which evidently subsists on the red matter, not yet taking in food from the outside; as a matter of fact there seems to be no distinct rectum as yet. Gradually the red colour disappears completely from the stomach, which in the fully formed larva is only of a faint yellow tinge.

The fully formed larva (Pl. IX. Fig. 3) is a quite typical *Ophiothrix* larva, distinguishable only by its peculiar coloration: a more or less irregular brownish-black spot above the stomach and a similar smaller spot off each corner of the preoral area, these latter spots being usually connected with that above the stomach by a

[1] Very probably it is this species which Koehler (Echinides, Astéries et Ophiures recueillis par M. Gravier dans la Mer Rouge. Bull. Mus. d'Hist. nat. 1905. 3) mentions under the name *Ophiothrix propinqua* Linné (erroneously for Lyman). As a matter of fact I have grave doubts as to the possibility of distinguishing *triloba* and *propinqua* from one another. The type locality of *triloba* is the Red Sea.

less clearly defined strand to each side of the oesophagus. These colour spots, which are usually very conspicuous, though subject to much variation, lie on the dorsal side of the larva. A faint reddish tint is found along posterolateral rod in its lower part; the arms are otherwise uncoloured.

The skeleton (fig. 34) is quite like that of other *Ophiothrix* larvæ; the body rods are slightly swollen. Usually there is no median process from the transverse rods, but in some cases a simple, styliform process is found. The posterolateral rods are sparsely set with small thorns along the inside.

The larvæ did not metamorphose, though kept till the end of June.

16. **Ophiomaza cacaotica** Lyman.

Pl. IX. Figs. 4—5.

A couple of specimens of this species were brought by the sailors on May the 30th, taken by dredging at a depth of about 20 m off Abu Sadaf, outside the station; no doubt they were attached to some Comatulids taken in the same place. Making a slit in an interradius of one of them I found it to be a ripe female, the eggs coming out isolated and apparently ready for fertilization. Finding another to be a ripe male, I tried to obtain artificial fertilization, but without success. Few minutes after, however, the female that had been slit open in one interradius shed by itself the rest of the eggs; I took then sperma from the other specimen and added to the eggs, and now fertilization followed immediately.

The eggs are of the usual small size, c. 0.1 mm., brownish, intransparent. By the cleavage a transparent layer is formed around the cleavage cells. The first divisions occurred after one hour, and the blastosphæra stage was reached after six hours in the evening, so that the further development could not be followed very closely. The

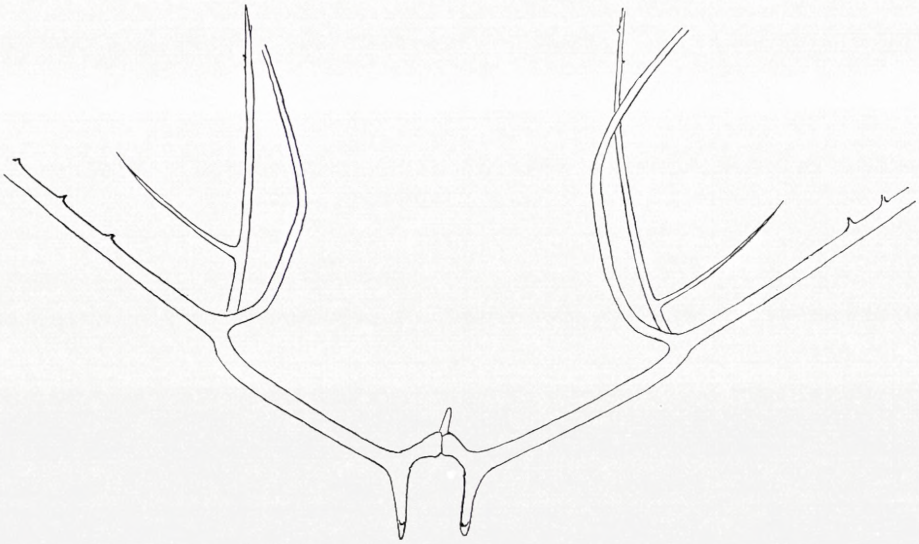
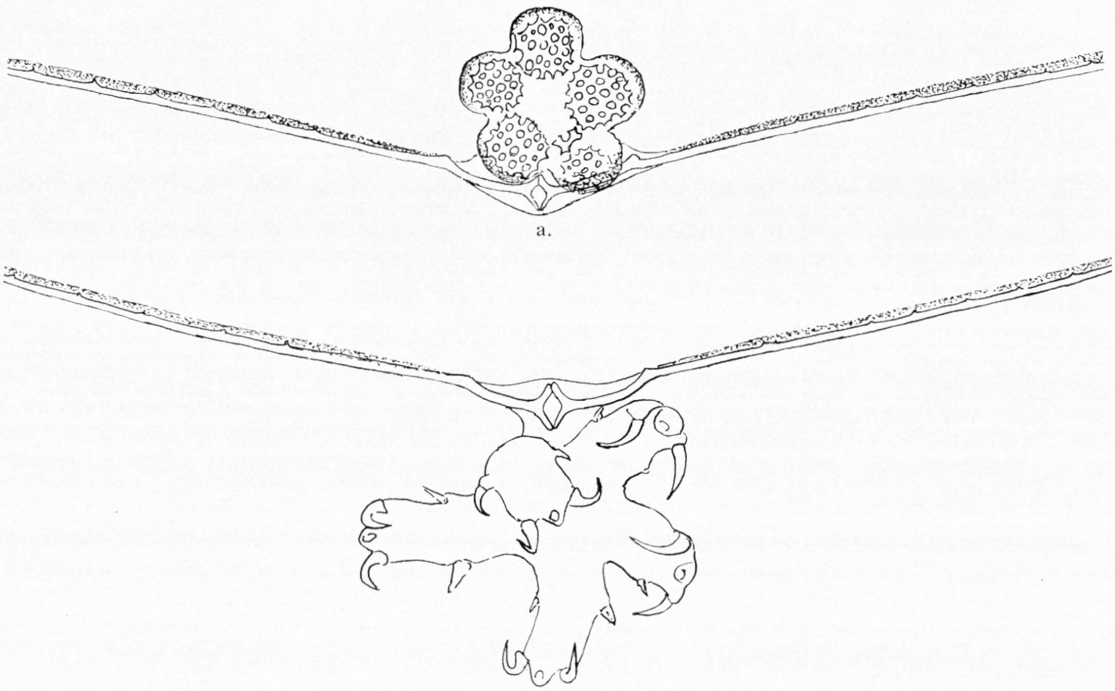


Fig. 35. Skeleton of the larva of *Ophiomaza cacaotica* Lym. × 250.

gastrulæ are rather elongate, pear-shaped, the anterior end being transparent, the broader posterior end dark, intransparent, evidently containing the yolk of the egg, whereas the clear cells of the anterior end, the "crest", are no doubt vacuolated, as described by MacBride (Op. cit.) in *Ophiothrix fragilis* (no sections have been made of them).

The larva had reached nearly full shape at the age of 5—6 days; it is remarkable in the enterocoel vesicles lying unusually far out towards the side, away from the



a.

b.

Fig. 36. Metamorphosing young *Ophiomaza cacaotica*, using the long posterolateral arms as a floating apparatus. Fig. b. shows the young brittle star about to detach itself from the floating apparatus. × 125.

stomach, and even in the later stages at the beginning metamorphosis (Pl. IX. Fig. 5) the enterocoel does not attach itself so closely to the stomach as is usually the case in Ophiurid larvæ.

The shape of the larva is that of a typical *Ophiothrix* larva, with long, nearly horizontally directed posterolateral arms. The colour is very faint; there is a small red spot in the end of the posterolateral arms and a little black pigment in the vibratile band along these arms. Along the body rods and the posterolateral rods is a faint yellowish-red tint, and the stomach is faintly yellowish; otherwise the larva is colourless. — The skeleton (fig. 35) differs from that of the *Ophiothrix* larva only in the body rods being longer and more slender, and the postoral rod characterically curved in the basal part. — It recalls that figured in my "Studies" 1921, p. 130, as *Ophiopluteus* of *Ophiothrix* species d, and leads to the suggestion that this larva also belongs not to the genus *Ophiothrix* itself, but to one of the other genera within the family of the Ophiothrichids.

Several of the larvæ metamorphosed, the metamorphosis beginning at the age of 12—14 days. I found the hydrocoel to grow round below the oesophagus, as it is figured for *Ophiothrix fragilis* by MacBride (Op. cit. Pl. 32, fig. 13, b). The metamorphosis on the whole proceeds exactly as in *Ophiothrix*, the long posterolateral arms remaining intact and serving as floating apparatus for the young brittle-star (figs. 36, a, b), then to be thrown off by completed metamorphosis and perish after having continued pelagic life for a little while. The young brittle-star has its armspines developed into long, simple claws. A curious fact is that in some cases there is no central plate in the young brittle-star (fig. 36, a).

It is very satisfactory to have thus ascertained that the *Ophiomaza* larva is a typical Ophiothrichid larva, a rather certain proof that we have a very distinct larval type characteristic of the family of the Ophiothrichidæ.

17. **Ophiocoma erinaceus** Müller & Troschel.

Pl. VIII. Fig. 4.

Ripe specimens of this species, which is fairly common on the reefs at the station, were found in the end of April, and spawned in the aquarium on April the 24th. The eggs are small, c. 0.1 mm., reddish, intransparent, and surrounded by a thorny fertilization membrane, which must undoubtedly be of some importance for keeping the eggs floating, as suggested in my "Studies" 1921, p. 131. That the eggs lie on the bottom in the dish, with no movement of the water, does not mean that the spiny egg-membrane cannot have such function in the free, where the water is in constant movement; it is also evident that they sink more slowly to the bottom

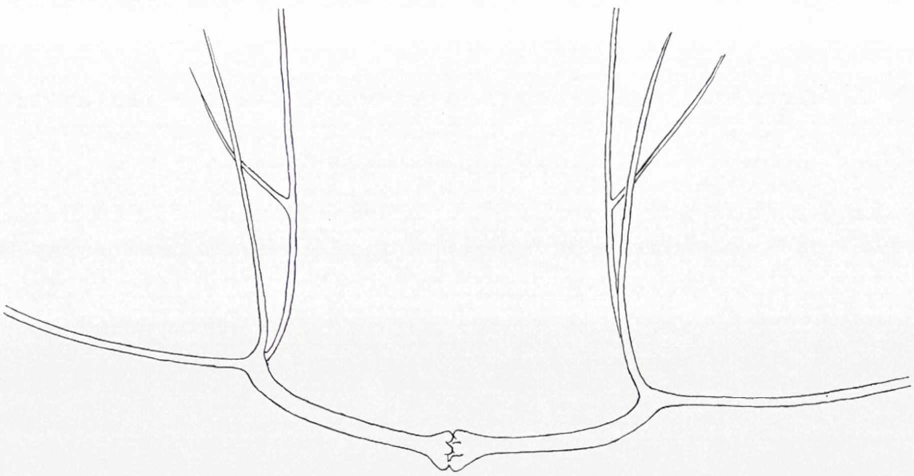


Fig. 37. Skeleton of the *Ophiocoma erinaceus* larva. × 250.

than eggs without such thorny membrane. I have no detailed observations of the development of the younger stages. The gastrula stage is reached after one day, the skeleton beginning to appear on the third day. At the age of six days the larvæ were exactly like the young *Ophiocoma echinata* larva figured in my "Contributions" 1931, p. 27, fig. 11. a, this larva being only $2^1/_2$ days old. Eleven days old the larvæ were exactly like the six days old *Ophiocoma echinata* larva figured in fig. 11. b of the "Contributions" 1931, p. 27. The development of this species thus takes about twice the time that does the development of *Ophiocoma echinata.* At the age of about a month the larvæ were nearly fully formed (Pl. VIII. Fig. 4), though not yet showing any sign of metamorphosis. They did not develop any farther.

The larva is colourless, only a dark-grey spot in the end of the posterolateral and anterolateral arms. Vibratile lobes are indicated; they will undoubtedly be more developed, when the larva is about to metamorphose. The strong upwards bend of the preoral band is not a reliable specific character, as it is subject to change in the live specimens. — The skeleton (fig. 37) is a quite typical *Ophiocoma* skeleton, the body rods lying horizontally, forming like a joint in the middle, where they meet. The skeleton is entirely smooth.

18. **Ophiocoma scolopendrina** (Lamarck).

Pl. VIII. Fig. 5.

This species is very common on the littoral reef-flat at the laboratory, their arms protruding from every crevice; often they are also seen crawling free in the small pools left at low tide. They were found to be ripe in the beginning of May (probably their breeding season begins at least as early as April), and some specimens spawned in the aquarium on May the 8th. The egg-membrane is thorny (fig. 38), as in other *Ophiocoma* species (but apparently not in *Ophiocomina nigra*, since nothing is said about it neither by myself, Op. cit. 1913, nor by Narasimhamurti, Op. cit.). It appeared that some of the embryos had difficulty in getting out of the egg-membrane (such as is so evidently often the case also in the Comatulids, cf. below, p. 61); this will most probably not occur in the free under natural conditions. The gastrulæ are elongate, intransparent. At the age of two days the first rudiments of the skeleton are seen.

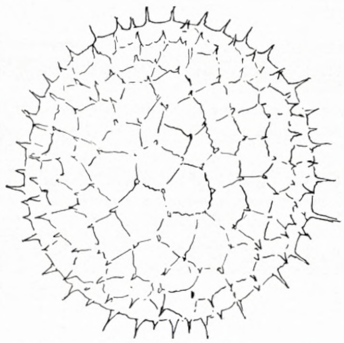


Fig. 38. Egg of *Ophiocoma scolopendrina.* × 540.

The young larvæ are very much like the *Ophiocoma erinaceus* larva, only the anterolateral arms somewhat larger. The one figured Pl. VIII. Fig. 5 was eleven days old, that of *O. erinaceus* five weeks old. Thus the development of the young stages passes much quicker in *scolopendrina* than in *erinaceus*; but the later development is slow, the metamorphosis having not yet begun at the age of six weeks, although the larvæ were apparently quite healthy.

The fully formed larva (fig. 39) has well developed vibratile lobes. The anterolateral arms are rather long; the anterior part of the body is somewhat widened.

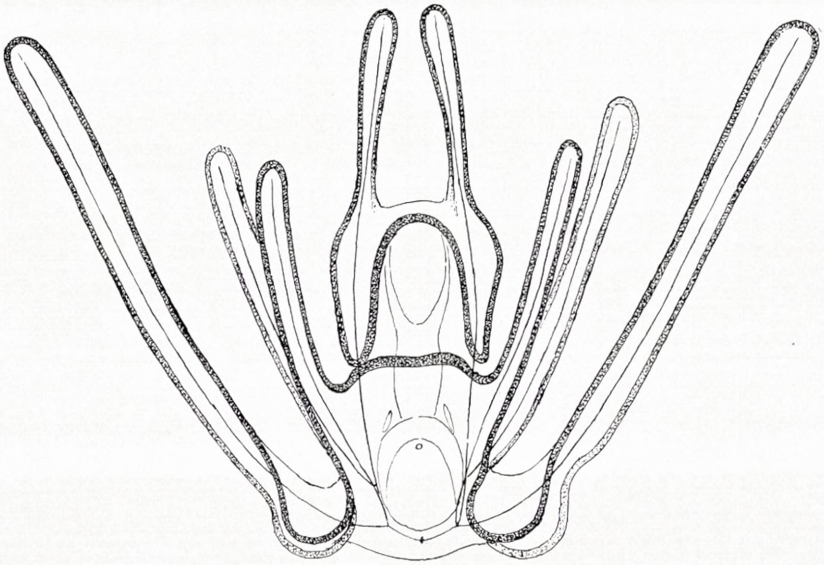


Fig. 39. Fully formed larva of *Ophiocoma scolopendrina*. × 70.

The strong upwards bend of the preoral band is, as in *O. erinaceus*, no reliable specific character, but may change actively in the live larva. The colour is a faint yellow, due to numerous small spots all over the body; in the end of the posterolateral arms

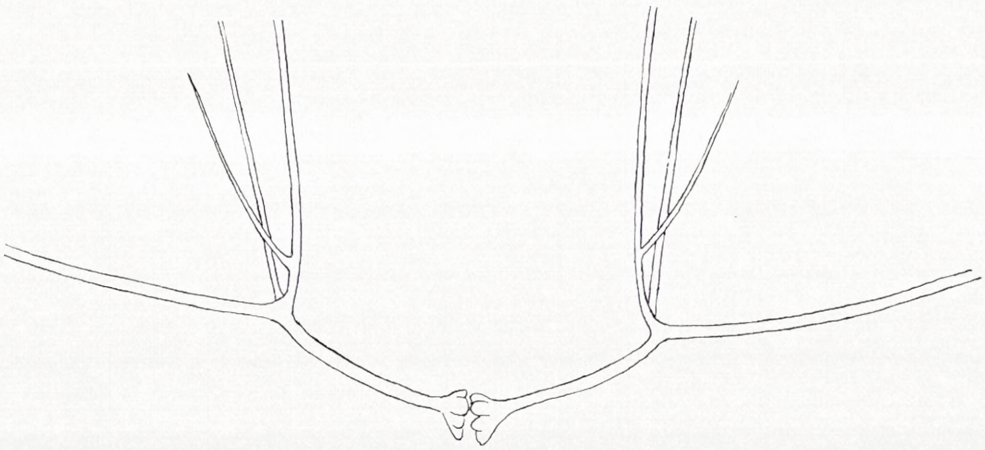


Fig. 40. Skeleton of the *Ophiocoma scolopendrina* larva. × 250.

there is a more conspicuous yellowish spot. The stomach also is a faint yellowish. — The skeleton (fig. 40) is as typical in *Ophiocoma* larvæ, hardly distinguishable from that of the *erinaceus* larva; only the body rods are slightly less horizontal.

19. **Ophiocoma lineolata** (Desjardins) Müller & Troschel.[1]

Syn. **Ophiocoma pica** Müller & Troschel.

Pl. VIII. Figs. 1—3.

The present species occurs, though not very commonly, on the reefs at Ghardaqa. Some specimens were brought me on May the 20th; they were put into a rather small dish in which they spawned during the night. The egg-membrane in not thorny, such as is the case in the species *Ophiocoma echinata*, *erinaceus* and *scolopendrina*; still the eggs are almost floating, on account of the presence in the surface layer of numerous small yellowish-brown yolk-granules; in the cleavage stages these granules form a beautiful mosaic, lying in the surface layer of the cells, but not along the cell-limits, only in the middle of the cells. The cleavage proceeds rather slowly; it appears that no blastosphæra is the result of the cleavage, but a solid morula; but the early development could not be followed in details because of the night. The first rudiments of the skeleton appear in the two days old embryos; but not until the age of six days have they assumed distinctly the shape of a young Ophiopluteus, as represented in Pl. VIII. Fig. 1, peculiar especially by the large size of the preoral part of the body, by the presence of distinct nerve-bands, and by the apparent slow development of the skeleton, the body rods having not yet reached to the posterior end of the body. In the course of the further development, however, the surprising fact was revealed that the body skeleton remains in a rudimentary condition, the body rods being simple, short, not reaching down to join in the posterior end of the body, and transverse rods being absent (fig. 41). On the other hand the rods of the arms are normally developed. This is a quite unique condition among normal plutei; in the few cases known, where the larva is reduced to a rudimentary condition, the body skeleton remains, whereas the arm-rods have disappeared (cf. "Studies" 1921, p. 229).

The larva in its further development is peculiar by the rather enormous size of the preoral part of the body, the anterolateral arms not being set off distinctly, the vibratile band only outlining the side edges of the large preoral part of the body (Pl. VIII. Fig. 2). In the fully formed larva, about a month old, the anterolateral arms have become differentiated, but they remain short and broad. There are now also distinct vibratile lobes as in the other *Ophiocoma* larvæ; the arms are rather broad and flat as usual in *Ophiocoma*. Rather characteristic of the larva is the large suboral cavity, distinct already in the youngest pluteus. The nerve-strands remain distinct also in the fully formed larva, as I have ascertained on the preserved specimens; (evidently I overlooked them when drawing the larvæ from life, and I have thought

[1] There can be no doubt that *Ophiocoma pica* and *lineolata* are identical, and most authors adopt the name *pica*, because it is placed first in Müller & Troschel's "System der Asteriden". But the name *lineolata* is the older, since it was given by Desjardins, as a manuscript name, and taken over by Müller & Troschel. As this name *lineolata* also gives the peculiar character of the species in the best possible way, so that one can, so to say, recognize it by the name, whereas *pica* says nothing, I think *lineolata* is the name to be used.

it better not to introduce them into the figures afterwards, the exact location being difficult to ascertain). The colour of the young larvæ is rather conspicuous: a number of yellow or orange spots along the vibratile band, especially in the end of the postero-lateral and anterolateral arms, and in the posterior part of the body. In the fully formed larvæ the colour is much fainter, though of the same yellowish tint.

A few of the larvæ metamorphosed; but I have not followed the metamorphosis in details on the living specimens, and the preserved specimens are insufficient for giving valuable information. Thus e. g. I cannot say whether the hydrocoel grows round above or below the oesophagus.

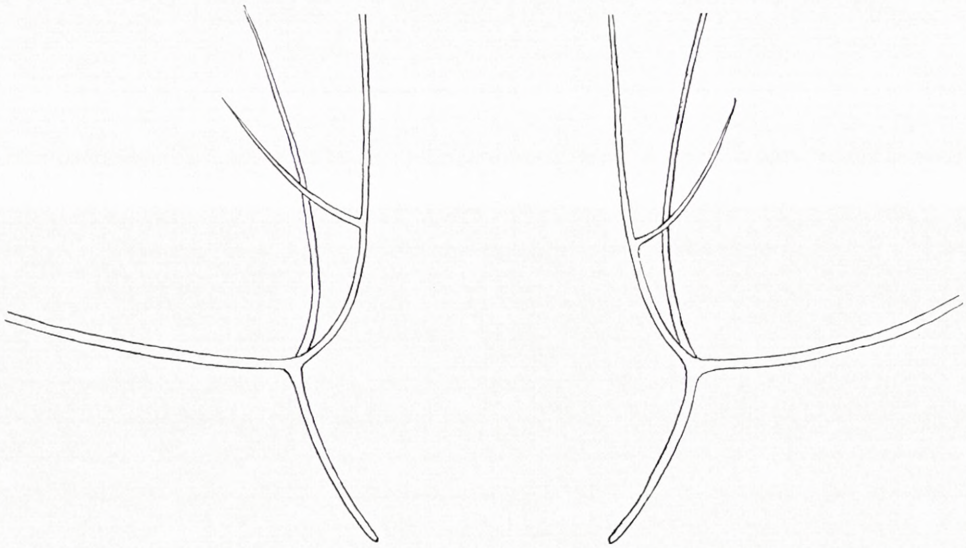


Fig. 41. Skeleton of the fully formed larva of *Ophiocoma lineolata*. No resorption has taken place, the body rods never joining in the posterior end of the body. × 300.

Although *Ophiocoma lineolata* differs conspicuously from the other *Ophiocoma* species in its coloration, it is surprising to find its larva to differ so much from the larvæ of the other species. One might even be tempted to conclude from the character of the larva that the species *lineolata* should be removed from the genus *Ophiocoma*. However, I do not think it advisable to do so, so long as we do not know the larvæ of all the various *Ophiocoma* species, and of the other genera of the Ophiocomidæ. As a matter of fact the *O. lineolata* larva to some degree recalls the larva of *Ophiocomina nigra*, and thus lends support to the general acceptance of this North-Atlantic Ophiurid belonging to the Ophiocomidæ, against H. L. Clark's idea that it belongs to the Ophiacanthidæ, even to the genus *Ophiacantha* itself, as set forth in his "Catalogue of the recent Ophiurans" where he even designates it by the quite unacceptable name *Ophiacantha sphærulata* (Pennant) (cf. my "Notes on some Scandinavian Echinoderms". Vid. Medd. Dansk Naturh. Foren. 72. 1920, p. 50—53).

Holothurioidea.

20. **Synaptula reciprocans** (Forskål).

Pl. X. Fig. 6.

This species occurs together with the following, *Synaptula vittata*, in great numbers on the shore flats at Ghardaqa. During day-time they usually hide themselves away under algæ and loose blocks of coral or stone in the small pools left by the tide, at sunset and early in the morning they come out and creep about like small snakes, the two species, one black, the other grey, striped, mixed together. It is surprising that they can stand the very high temperature that prevails in these localities at low tide under the glare of the sun.

A number of specimens were put together into a big dish on May the 19th and spawned during the night. The eggs are very small, only c. 0.05 mm. Early in the morning they were blastulæ, though not yet free-swimming; in the course of the day, scarcely more than some 18 hours old they were gastrulæ, rather elongate, but otherwise quite typical. On the next day the mouth had been formed, but the Auricularia shape was still hardly indicated and only the first traces of the postoral and preoral vibratile bands were to be discerned. Three days old they were young Auricularias, exceedingly clear and transparent, and with 1—3 small spheres in one of the postero-lateral corners. At the age of about two weeks they were apparently fully formed larvæ, with a number of small wheels scattered over the body. Beyond this stage they did not develop, though kept alive for another week.

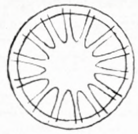


Fig. 42. Wheel of Auricularia of *Synaptula reciprocans*. × 240.

The larva (Pl. X. Fig. 6) is of very simple shape, merely with a fold on the middle of the band along the dorsal side. Seen in side view it is very thick in the anterior part, with the postoral area somewhat projecting, as a lip, like the following species, cf. Pl. XI. Fig. 6. The larva is perfectly clear, without the slightest trace of colour. — The wheels are of a quite simple type, with 12—13 spokes (fig. 42).

21. **Synaptula vittata** (Forskål).

Pl. X. Fig. 7; Pl. XI. Fig. 6.

As stated above this species occurs in great numbers together with *S. reciprocans* on the shore flats at Ghardaqa, under the same life conditions. A good number of specimens were put into the tank of the laboratory with some of the algæ among which they usually occur, and here they lived very well for some days and spawned during the night of June the 6th.

The eggs are like those of *S. reciprocans*; the first development stages offer the unusual feature that gastrulation begins already before the embryos have left the egg-membrane. Otherwise there seems to be no difference from *S. reciprocans*. (I did not observe whether the gastrulation of *S. reciprocans* starts before the embryo leaves the egg-membrane). The larva (Pl. X. Fig. 7; Pl. XI. Fig. 6) is very clear and transparent, without any trace of colour, very thick in the anterior part. As in *S. reciprocans* there are 1—3 spheres in the left posterolateral lobe, and in the later stages a number of Auricularia-wheels scattered irregularly over the body. The nerve strands are very distinct, as is also the oesophageal vibratile band, the adoral band, as it was termed by Semon, who was the first to describe it (Die Entwickelung der Synapta digitata und ihre Bedeutung für die Phylogenie der Echinodermen. Jen. Zeitschr. XXII. 1888. p. 125).

The figure of this larva shows it to be more folded than that of *S. reciprocans*; this, however, is probably due to some difference in age, and it is to be expected that the latter larva will be just as much folded in the later stages as is the *S. vittata* larva — and very probably both of them will be still more complicately folded by the time metamorphosis sets in. Among the larvæ of *S. vittata*, preserved the last day before my departure — thus three weeks old — I find one specimen very much more folded, and with a great number of wheels all over the body. Unfortunately the anterior end of it has been destroyed, so I cannot give a figure of it — the more so as the fact that there are no spheres in the posterolateral lobe makes me a little uncertain, whether it is really the same species, and not one which has happened to be in the water from the outside. But in any case it is a Synaptid larva.

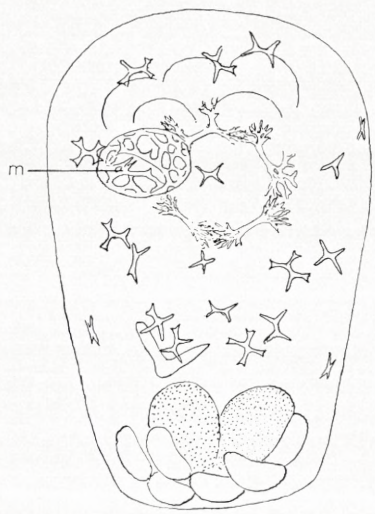
This said larva approaches to some degree the famous *Auricularia nudibranchiata* of Chun and makes it probable that this fine Auricularia does really belong to some Synaptid, as suggested by MacBride and recently by Densaburo Inaba (On some Holothurian larvæ and young from New Guinea. Bull Jap. Soc. Scientif. Fisheries. II. 1934, p. 213). One might be tempted to suggest that it belongs to the large Synaptids of the genus *Synapta* or *Opheodesoma*; in any case it would be of the greatest interest to study the development of these gigantic Synaptids. Unfortunately my efforts to induce the *Synapta maculata* Ch. & Eyssenh. and *Opheodesoma serpentina* (Joh. Müller), found in fair numbers near Ghardaqa, to spawn were not crowned with success, although I had a good number of them living for some time in the tank. Artificial fertilization, which I also tried, did not succeed either. Possibly it was too early for their breeding, although the eggs seemed to be ready for spawning.

22. **Stichopus variegatus** Semper.

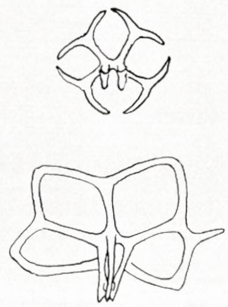
Pl. XI. Figs. 1—5.

Owing to the peculiar property of *Stichopus* (at least some species of the genus) that its skin dissolves when it is kept under unnatural circumstances, I had much trouble in getting the development of this species, which is rather common at the reefs near the station. But finally during the night of June the 20th some specimens spawned in the tank of the laboratory. By the time I left Ghardaqa, June the 27th, the embryos were only young Auriculariæ; but after my departure Zaky Effendi looked after the culture in the most excellent way till the end of July, preserving specimens in the various stages. On the material received from him I could then follow the development until the young Holothurian. As the larva is perfectly colourless, nothing was lost either in regard to colour by having only preserved material for study.

When observed in the morning of the 21st the embryos were already in the blastula stage; they were very clear, rather unusually large (I have forgotten to note anything about the size of the eggs). On the next day they were beginning to assume the Auricularia shape; on the third day the first rudiments of the spicules in the posterolateral corners were seen, but the Auricularia shape was not fully assumed till the fourth day.



43.



44.

Fig. 43. Young Holothurian of *Stichopus variegatus.* × 240. m. madreporite.
Fig. 44. Spicules from young *Stichopus variegatus.* × 300.

The young Auricularia (Pl. XI. Fig. 1) is very simple; it differs from the *Holothuria* larva in having a spicule in each posterolateral corner, but no spicule or sphere in the middle of the hind end. The spicule is irregularly star-shaped. In the fully formed larva, before beginning metamorphosis (Pl. XI. Figs. 2, 4), the vibratile lobe forms a small postoral fold or lobe and a larger, more complicate dorsal fold resulting ultimately in the formation of a rather distinct antero- and posterodorsal lobe. The posterolateral corners are produced into more distinct lobes, in each of which a granular mass has appeared. The spicules may sometimes be entirely absent, sometimes only one of them is present, but normally there is one in each posterolateral lobe. The nerve strands are distinct. The enterocoel has begun to grow downwards. In one larva of this stage there is a double hydrocoel, with a common hydropore; here a small separate enterocoel vesicle lies below the stomach (Pl. XI. Fig. 3). A granular sphere is seen in the right anterodorsal lobe.

In the next stage (Pl. XI. Fig. 4) the hydrocoel has developed the primary lobes, and the madreporite, with its calcareous skeleton, is distinct, and the large, transparent, elastic balls have appeared in the posterolateral and the two dorsal lobes; in one of the anterolateral corners a similar ball is found, but not in the other. These anterolateral balls are not of constant occurrence; thus in the metamorphosed specimen, Pl. XI. Fig. 5, there are only three balls to each side, both the anterolateral ones lacking. Below the ball in the posterolateral corners is seen the granular mass.

The metamorphosed young (Pl. XI. Fig. 5) has the typical barrel-shape, with five vibratile bands. Beside the posterior balls are seen the larval spicules, and then under the granular masses are seen a number of small glassy disks. These are seen more developed in the more advanced stage fig. 43. Here the balls have disappeared, but the granular bodies still remain distinct; it would appear that they have something to do with the formation of the glassy disks, which are here seen to have a lenticular shape, a little concave on the side turning inwards. There is still a trace of the larval spicule, but then the formation of the spicules of the body wall of the Holothurian has begun; the madreporic skeleton is finely developed, and the five radialia of the calcareaous ring have appeared. In a slightly more advanced specimen the body spicules are beginning to assume the shape of tables (fig. 44). In this latter specimen only two of the glassy disks are left, one of them much reduced in size, and the granular masses are no longer distinct. It thus appears that both these bodies, the disks and the granular masses, have some kind of function only for the metamorphosing Holothurian, as must also be the case with the elastic balls, which likewise have disappeared by the time the calcareous ring and the spicules of the Holothurian have appeared.

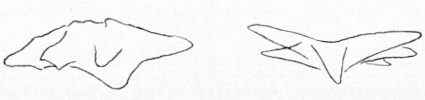
The only other *Stichopus* larva known, that of *Stichopus californicus* (Stimpson) (cf. my "Studies" 1921, p. 196, Pl. XXXIII. 8—9) agrees with the present larva in having an irregular, star-shaped spicule in each posterolateral corner, but nothing in the middle of the hind end of the body. It would appear thus that this is a character distinguishing the *Stichopus* larva from the *Holothuria* larva. In the shape of the larval body there is no difference between the larvæ of these two genera.

23. **Actinopyga serratidens** Pearson.

Pl. XIII. Figs. 1—3.

Some specimens of this species, which is common on grass bottom at a depth of c. 10 m. near the station, were put into a big dish at 7 o'clock in the evening of May the 19th. After an hour I found them in the act of spawning. They raise the anterior end when shedding the sexual products, but I did not observe this species to move the upraised part to the sides, such as was the case with *Holothuria* (*Bohadshia*) *marmorata* Jäger.

The development proceeds rather slowly. The gastrula stage is reached about 18 hours after fertilization; at the age of one and a half day the mouth is only just beginning to form, and not until the fourth day I found the embryos to be typical young Auricularias with beginning formation of a spicule in the posterior end of the body. In this stage they remained nearly unaltered for about two weeks (Pl. XIII. Fig. 1). The vibratile band is quite simple, forming only a small lobe on the middle of the dorsal side. A number of distinct yellow spots are found, almost symmetrically arranged, in the band all round. The nervous strands are very distinct. The calcareous body in the posterior end is an irregular star (fig. 45, a).



a. b.

Fig. 45. Calcareous spicule in the posterior end of *Actinopyga serratidens* (a) and of *Actinopyga mauritiana* (b). × 300.

In larvæ about three weeks old (Pl. XIII. Fig. 2) the metamorphosis is beginning, the hydrocoel has begun to form lobes, and the enterocoel vesicles are prolonging backwards. The larva has now the usual folds very well developed, and elastic balls have been formed in all the lobes, besides one in the middle of the posterior end, above the calcareous body, which has developed into a finely spiny sphere. The yellow spots of the vibratile band are fairly distinct, and small yellow spots scattered on the body.

At the age of nearly four weeks several of the larvæ had metamorphosed, the young Holothurians having the usual barrel-shape, with five vibratile bands and five pairs of elastic balls, besides the one in the posterior end (Pl. XIII. Fig. 3). The fifth pair of balls, which I did not observe in the larva, evidently develops in the slight dorsal fold below the anterior end.

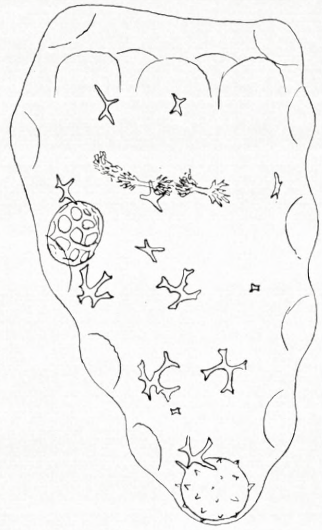


Fig. 46. Young Holothurian of *Actinopyga serratidens.* × 225.

In the oldest specimens obtained, four weeks old (fig. 46), the spicules of the body wall have begun to form, and the radials of the calcareous ring have appeared. The elastic balls are about to disappear, but the sphere in the posterior end is still in full shape.

24. **Actinopyga mauritiana** (Quoy & Gaimard) (Var.).

Pl. XIII. Fig. 4.

On May the 22nd the sailors brought home a number of specimens of this species from the outer reef. They must have spawned at once on being put into the tank, numerous blastulæ being found already at 9 o'clock in the evening. I have no detailed observations concerning the development processes.

Pl. XIII. Fig. 4 represents an 8 days old larva, evidently fully formed, but not yet in beginning metamorphosis. The larva has an irregular star-shaped spicule (fig. 45. b) in the middle of the posterior end, which is not produced — a character which distinguishes this larva from the *Holothuria* larvæ, in which the middle of the posterior end, containing the spicule, is usually produced. Apart from this feature and the different shape of the spicule these larvæ are otherwise closely alike.

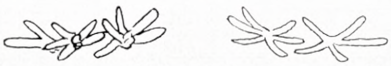
As was to be expected, the larva of the present species agrees very closely with that of *Actinopyga serratidens* in the character of the spicule, in the young larval stage. Whether it will develop into a spiny ball in the later stages also of the present species remains to be seen; if so, we may have herein a character peculiar to the *Actinopyga* larva.

The larvæ did, unfortunately, not develop beyond the stage figured; I have thus also been unable to ascertain whether elastic balls will be present in the metamorphosis stage; but there is, of course, no reason to doubt that they will be formed here as in other Aspidochirote larvæ.

25. **Holothuria (Bohadschia) marmorata** Jäger.

Pl. XII. Figs. 5—6.

This species is common on grass bottom at a depth of c. 10 m at the station. It is highly variable in colour, so that at first I took it for being two different species and therefore got two different cultures of the larvæ, on May the 12th and May the 19th. The fact that the larvæ in both cultures were exactly alike testifies the correctness of regarding all the colour variations as merely individual variations. The more general colour was a more or less dark brown on the dorsal side, the ventral side being somewhat lighter. The larger specimens, when caught in the trawl, usually assumed a shape almost exactly like a football; when put into the tank of the laboratory they again assumed the normal sausage-shape. As described above (p. 9—10) this species raised the foreend of the body when spawning, spreading it out and flattening it, the genital papilla coming out quite distinctly. It moved the foreend to the sides during the spawning.



a. b.

Fig. 47. Spicules of the *Holothuria marmorata* larva, a. from the middle of the hind end, b. from the right posterolateral lobe. × 300.

At the age of c. 12 hours the embryos were blastulæ, rotating within the egg-membrane, which latter I observed to be much swollen, slimy (but sharply limited on the inside); it looked as if this would serve as a floating apparatus. One and a half days old they were beginning to assume the Auricularia shape. At the age of four days the formation of the spicules had begun. None of the larvæ reached the metamorphosis stage.

The larva (Pl. XII. Figs. 5, 6) does not show any peculiar features in regard to shape, but in its spicules it differs very markedly from the other *Holothuria* larvæ reared. The spicules are slightly irregular stars, generally with 5—6 rays (fig. 47). They are found both in the middle of the posterior end (which is not produced) and in all the lobes, varying in number from 1—3 in the posterior end and in the posterolateral lobes, usually only one in the other lobes (probably more in older larvæ). The rays of the stars may be distinctly curved so as to resemble wheels in formation. The colour is a very faint yellowish on the body, more distinct yellowish spots on the vibratile band. — The nerve strands were rather indistinct.

None of the larvæ reaching beyond the stage figured, I cannot say whether the elastic balls will be found in the metamorphosis stages; but it may well be expected that they will be found here as in the other larvæ.

26. **Holothuria arenicola** Semper, var. **Boutani** Hérouard.

Pl. XII. Figs. 3—4.

The present species occurs very commonly in the sand on the flats near the station, buried rather deep down, not visible on the surface; also under the stones on the flat it is found quite commonly. Some specimens were put into a large dish, without sand, on May the 21st, and spawned during the night. The embryos were in the gastrula stage already next morning. I have no detailed information of the development processes.

The young larva (10 days old), Pl. XII. Fig. 3, is of the usual shape. In the middle of the posterior end lies, in a distinct prominence, a rounded, lobed, calcareous spicule (fig. 48); sometimes, as in the specimen figured, it lies unsymmetrically. The larvæ near metamorphosis (Pl. XII. Fig. 4), about four weeks old, have elastic balls present in all the lobes, also one in the posterior end, above the spicule; no balls were seen as yet in the anterolateral corners, but no doubt they will develop there before metamorphosis. — The larva is very transparent, with only some small yellow spots in the vibratile band and a very few similar spots scattered on the dorsal side (none on the ventral side).

Fig. 48. Spicule from the posterior end of the larva of *Holothuria arenicola.* × 300.

A few of the larvæ had transformed at the age of four weeks. The young Holothurians were opaque, yellowish-grey, the number of balls being not distinctly observable. On specimens cleared in Canada balsam (fig. 49) it seems that there are five pairs, but they are not very distinct. The madreporite skeleton is very well developed, the calcareous ring and the first spicules have appeared. The calcareous body in the posterior end is conspicuously larger than in the larvæ, a rather curious fact indicating that this spicule may perhaps persist for some time in the young Holothurian; it would be interesting to follow its fate during the further growth of the young Holothurian.

Fig. 49. Young Holothurian of *Holothuria arenicola.* × 250.

27. **Holothuria scabra** Jäger (**H. tigris** Selenka).

Pl. XII. Figs. 1—2.

This species, usually very strikingly coloured, with narrow white transverse bands on the dorsal side, is common on grass bottom, at a depth of c. 10 m, near the laboratory. Specimens were repeatedly put into the tank in the hope that they would spawn, but without success. Once I tried to induce them to shed their sexual products by making a slit in the body wall — a proceeding which I have on some occasions found to lead to the desired result — but still nothing happened. Finally, on June the 8th, when I had again put several specimens into the tank, I had the pleasure of finding the next morning numerous gastrulæ in the water, which gave a very good culture. On the next day they had assumed the shape of young Auriculariæ, without special features. Five days old the larvæ had the shape as represented in Pl. XII. Fig. 1, characteristic by a long median prominence of the posterior end, in which lies a calcareous sphere. This sphere is smooth in the present stage, but I found its surface a little uneven in younger larvæ. The prominence was generally somewhat unsymmetrically placed. The nerve strands were very conspicuous, and with a distinct nerve proceeding towards the dorsal vibratile band (this nerve appears to be a constant feature of the Auriculariæ). The oesophageal band is unusually broad and has the appearance of being also of nervous structure.

At the age of 18 days I found the larvæ near metamorphosis and with elastic balls beginning to appear (Pl. XII. Fig. 2). The shape of the fully formed larva is quite as usual. The colour is the usual, faint yellow spots along the vibratile band and a few along the posterior end. — The larva figured was abnormal in having a right, not a left hydrocoel.

None of the larvæ metamorphosed.

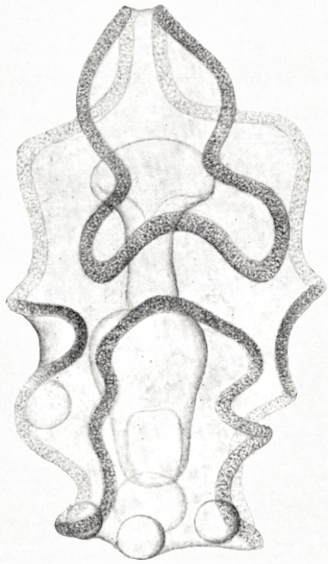


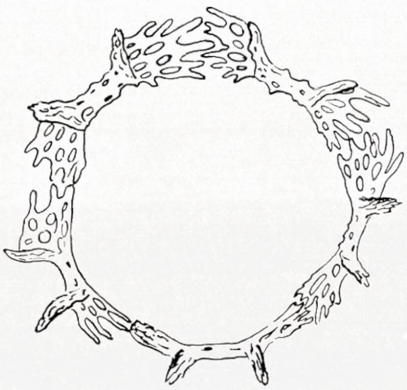
Fig. 50. Auricularia of *Holothuria spinifera*, showing beginning formation of the elastic balls. × 200.

28. **Holothuria spinifera** Théel.

Pl. XIII. Fig. 5.

A number of specimens of this species were put into the tank on June the 18th, and were observed to spawn at 6 p. m. At 8—8.30 p. m. the eggs were in the 2—4 cells stage. 14 hours old they were blastopheres, but not yet moving, within the egg-membrane. At 17 hours they were rotating within the egg-membrane, having already assumed the gastrula shape; at 18—19 hours they were free-swimming. In the course of the second day the embryos began to assume the Auricularia shape, and on the third day the spicule in the posterior end had begun to form.

Pl. XIII. Fig. 5 represents a larva 8 days old. It is of the typical young Auricularia shape, and has a smooth calcareous sphere in the middle of the posterior end in a small prominence. Sometimes there may be two or even three of these spheres. The colour is the usual: small faint yellow spots in the vibratile band and in the posterior end.



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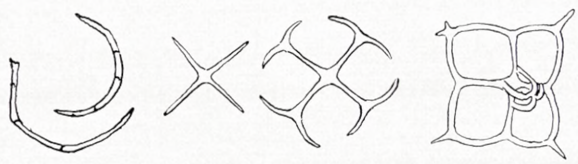


a. b. c. d.

52.

Fig. 51. Calcareous ring (radials) of young *Holothuria spinifera*.

Fig. 52. Spicules from young *Holothuria spinifera*; a. from the tentacles; b—d. developmental stages of spicules (tables) from the skin. All × 300.

After my departure from the laboratory ZAKY EFFENDI looked after the culture and sent me the preserved specimens of the metamorphosis stages. As seen from fig. 50, elastic balls are present (still only beginning to form in the specimen figured). A couple of specimens had metamorphosed; the calcareous ring (radials), and also the first spicules of the body wall and of the tentacles have been formed (figs. 51—52). The skeleton of the madreporite is of the usual type, an irregular network. The elastic balls are not visible.

Crinoidea.

29. **Tropiometra Audouini** A. H. Clark.

Pl. XIV. Figs. 1—2.

This Comatulid, which occurs in good numbers on the reefs close to the station, mainly on the underside of old, loose coralblocks, was found ripe by the end of April. Some specimens were put into a large dish on the 18th and the next morning a good number of eggs were found lying on the bottom of the dish. The egg-membrane is spiny as in *Tropiometra carinata* (cf. my "Studies on the development of Crinoids". Papers from the Department of Marine Biology, Carnegie Inst. Washington. XVI. 1920). About 24 hours old the embryos were partly free-swimming, and on the next day there were some hundreds normal larvæ, with ciliated bands and vestibulary invagination. A number of embryos were still enclosed within the egg-membrane; it seemed clear that they had considerable difficulty in getting out of the shell in the still water in the dish, as I have formerly found it to be the case with *Antedon petasus* (cf. my "Notes on the development and the larval forms of some Scandinavian Echinoderms". Vid. Medd. Dansk Naturh. Foren. 71. 1920, p. 151). I then put these embryos into a plankton net in the tank, under the tap, so as to have them in constant movement in the water, and in this way I succeeded in getting another good lot of free-swimming embryos.

All the embryos were then put into some dishes with the bottom covered by small pieces of broken shells and corals, to which I hoped to see them attach themselves. Not till the 25th, thus after 5—6 days free-swimming, did I find a few of them attached and having assumed the Pentacrinoid shape; by May the 1st there were some 30 Pentacrinoids, all the rest of the larvæ still swimming, and no more of them did attach themselves. In the course of the following five days a few larvæ tried to attach themselves to the bottom of the dish, but without success, and in 2—3 days more all of them had disappeared. Evidently the difficulty with these Crinoid larvæ is to find suitable objects for them to attach themselves to, as I found it to be the case with *Tropiometra carinata* (cf. my "Studies in the development of Crinoids", p. 5).

Having already studied the embryological development of *Tropiometra carinata* in detail (Op. cit.), I did not preserve any of the larvæ for sectioning, wanting to have as much material as possible for eventually studying the further postembryonal development of the Pentacrinoids. I expected that by means of the various cultures of food-organisms that I had at disposal it would be easy enough to keep the Pentacrinoids growing in the dishes. Unfortunately, this did not prove successful. Repeated attempts to get new cultures of the larvæ failed; evidently the breeding season had passed — at least no more eggs were got. Thus the information I can give of the development of this *Tropiometra* species is confined to the above statements, and to the figures of the young Pentacrinoid.

This Pentacrinoid (Pl. XIV. Figs. 1—2) has much resemblance with that of *Tropiometra carinata* (Op. cit. Pl. X. Figs. 6—8). The oralia have no outturned edge, such as is found in the Pentacrinoids of the Antedonids. There are three well developed infrabasalia. The anal plate has appeared (Pl. XIV. Fig. 2), but there is no trace of the radial and neither have I found the spicules of the tentacles or the first sacculus in any of the Pentacrinoids, though kept alive till the age of three weeks. It may, however, be mentioned that as in *Tropiometra carinata* (Op. cit. Pl. X. Fig. 6) I have found in one specimen a small, young plate lying some distance out in the primary tentacle. It may be suggested that it is the first axillary; but in the absence of further development stages this remains a little uncertain.

30. **Lamprometra Klunzingeri** (Hartlaub).

Pl. XIV. Figs. 3—8; Pl. XV. Figs. 1—10.

This very beautiful Crinoid is common on the reefs at Ghardaqa, but not found under the loose blocks like *Tropiometra*. As a matter of fact they are not easily discovered at day time; but at sunset they come out from their hiding places and crawl up on top of the corals and sit there fully expanded, as big flowers. In places they may be found in good numbers and then afford a most gorgeous sight.

On May the 1st a number of specimens were put into a big dish, under a moderately running tap, and the next morning I had the pleasure of finding a number of eggs lying on the bottom of the dish. As the specimens were evidently in very good condition I kept them in the dish for eventually getting some more eggs from them. During daytime nothing happened, but in the evening a new spawning took place. By careful observations the following days I could ascertain that spawning takes place almost exactly at 7 o'clock in the evening.

The eggs are small, c. 0.1 mm., and the egg-membrane spiny as in *Tropiometra*. 14 hours old some of the embryos were free-swimming, the others rotating within the egg-membrane. Also in this species the embryos had difficulties in rupturing the egg-membrane in the dishes with the still-standing water; when put into a plankton-net in the tank, and the water from the tap running through the net, a much larger percentage of the embryos became free-swimming.

The embryos, when leaving the egg-membrane, are uniformly ciliated all over, but almost immediately the arrangement in distinct bands begins. In embryos one and a half day old there were four distinct bands and an apical tuft of longer cilia. They have a well developed sucking disk and are apt to attach themselves to the bottom of the dish; they are rather strong swimmers and show some positive phototropism. The skeleton of the Pentacrinoid has already begun to form (Pl. XIV. Figs. 3—4).

Like the *Tropiometra* larvæ the *Lamprometra* larvæ were put into dishes with the bottom covered by fragments of shells and corals, and also some algæ (*Halimeda*, *Sargassum*, etc.). On the 5th I found some 50 specimens attached and about to assume the Pentacrinoid shape; on the following day some few more had attached themselves, but the great majority (several hundreds) were unattached. I tried then to put some small pieces of floating *Posidonia* leaves into the dishes, and to put gravel on the bottom of the dishes for making it appear more like the natural sea-bottom — but with negative result; a few larvæ attached themselves to the glass itself, more or less successfully — but the great majority of the larvæ remained free-swimming till 11—12 days old, some of them in the shape of "hump-backed" Pentacrinoids, as described for *Tropiometra carinata* (Op. cit. Pl. IX. 5—6). Then they died off, without attaching themselves.

This curious fact observed now in three different species of Comatulids that the larvæ will not attach themselves, but remain swimming for several days, must, evidently, be of importance as a means of dispersal (cf. Op. cit. p. 4); but one cannot help thinking whether perhaps also under natural conditions numbers of the larvæ do not succeed in finding a suitable place for attachment. If they did all succeed in attaching themselves, one would expect young specimens of the Comatulids to be very common, in accordance with the enormous number of eggs produced. But, as a matter of fact, young specimens are almost not to be found; of course, they are difficult to see — especially the Pentacrinoids, but will that difficulty alone account for their scarcity?

As was the case with *Tropiometra* the Pentacrinoids would not thrive in the dishes, in spite of the adding of *Nitzschia*, *Chlamydomonas*, and other food-organisms, or of giving them fresh sea-water daily. An attempt to keep them in the tank with running sea-water did not succeed either. Wishing then to try to rear the Pentacrinoids by putting them out on the reef in such a way that they could be found again, I wanted to start some new cultures of the larvæ; but now the breeding season evidently was over; repeated attempts with new specimens of the Comatulid put into dishes, like done at first, gave no results. Thus the postembryonal development, beyond the first Pentacrinoid stage, could not be studied of this species either. A method for rearing the Pentacrinoids till the Comatulid stage has still to be found.

A fair number of larvæ of various ages were preserved (formol-sublimate) in order to be sectioned, as it would be of considerable interest to see, whether this representative of the family Mariametridæ would differ from the other forms, the development of which has been studied in detail, viz. *Antedon*, *Isometra*, and *Compsometra* of the Antedonidæ, and *Tropiometra* of the Tropiometridæ. (*Notocrinus*, of the family Notocrinidæ, is so highly specialized, and moreover the first stages unknown, that a direct comparison with the present form is hardly possible; cf. for *Compsometra*, *Isometra*, *Tropiometra*, and *Notocrinus* my "Studies in the development of Crinoids". 1920).

Unfortunately, the preservation of the embryos of *Lamprometra* is not all that could be desired, as a matter of fact not nearly as good as that of the above named forms, previously studied, preserved simply in alcohol. To this comes the difficulty caused by the very small size of the nuclei, particularly those of the ectoderm. I cannot, therefore, give a detailed description of the whole development, particularly as concerns the pore-canal and the enterocoel cavities. But so far as can be seen there is herein no essential difference from *Tropiometra*. In regard to the younger stages, however, there is a very remarkable difference between *Lamprometra* and the other forms, the corresponding stages of which are known, and these stages are, fortunately, sufficiently well preserved so that no doubt can obtain as to the correctness of the results.

The cleavage is perfectly regular, as seen from Pl. XV. Figs. 1—2; the 4-cell stage is reached already after two hours. Embryos four hours old have already reached the blastula stage, but the blastocoel cavity is completely filled by cells, which have wandered in, or budded off from the ectoderm (Pl. XV. Fig. 3). Sections of embryos 6—10 hours old show them still having the blastocoel cavity completely filled up by mesemchyme cells, lying close together, pressing each other into irregular polygonal shapes (Pl. XV. Fig. 4). There is no trace of a gastrula invagination and no gastrula mouth, and such is not seen either in the later stages; the gastral cavity develops as a sort of schizocoel by some of the cells of the blastocoel cavity arranging themselves so as to form an epithelium, limiting a cavity (Pl. XV. Figs. 5—6).

It is very interesting to compare this peculiar origin of the entoderm in *Lamprometra* with the way it originates in *Tropiometra* (cf. my "Studies in the development of Crinoids" p. 8; Pl. II. Fig. 2). Here the blastocoel cavity is nearly filled up with mesemchyme cells, before the gastrula invagination takes place, and the mesemchyme cells then arrange themselves on the top of the archenteron and participate in the formation of the entoderm. *Tropiometra* thus represents an intermediate step in regard to the entoderm formation, from *Antedon*, with a typical gastrula invagination, to *Tropiometra*, with the entoderm formed partly by mesemchyme cells, partly by a regular gastrula invagination, to *Lamprometra*, without any gastrula invagination, the entoderm formed solely by mesenchyme cells. (It may be incorrect to designate these cells filling the blastocoel cavity as "mesenchyme" cells. I do not attach any special importance to the use of this designation for these cells; it is merely for giving them some designation, without entering on a discussion of what might be a more appropriate term).

In embryos 22 hours old (Pl. XV. Fig. 7) the gastral cavity has divided into a lower and an upper part, the enterocoel and the hydrocoel vesicle; the vestibulum is beginning to form. In embryos $1^1/_2$ days old (Pl. XV. Figs. 8—9) the vestibulum is formed; the enterocoel is dividing into a right and a left vesicle, and the stomach has begun to differentiate. Finally Pl. XV. Fig. 10 shows the beginning closure of the vestibulum and the beginning formation of the chambered organ. The details about the pore canal could not be made out.

Attention may be called to the fact that the ciliated bands are not distinctly recognizable in the sections, such as I found them to be in *Tropiometra*; this may, partly at least, be due to the unusually small size of the nuclei.

The young Pentacrinoids are remarkable by the relatively large size of the anal plate (Pl. XIV. Figs. 5, 7). The oral plates are in the main as in *Tropiometra*, without outturned edges. There are no infrabasalia, as I have ascertained by very carefully dissolving some calyces under the microscope; neither is there any trace of infrabasalia observable in the embryos. This is then a conspicuous difference from *Tropiometra*; but, as I have pointed out in my "Studies in the development of Crinoids" pp. 75—76, the presence or absence of infrabasalia seems to be of no primary importance.

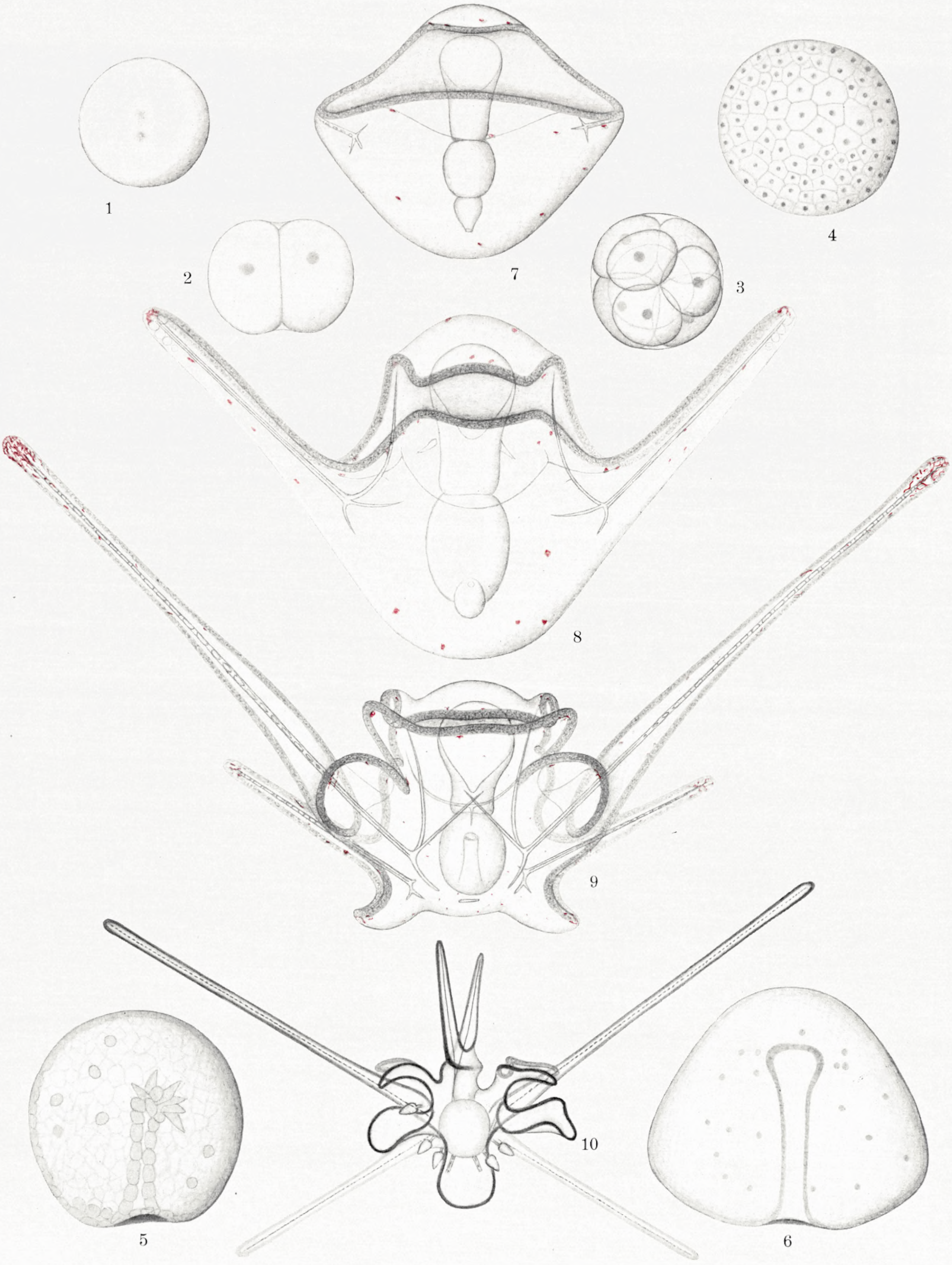
In the 6 days old Pentacrinoid Pl. XIV. 7 the mouth has just opened. Pl. XIV. 8 represents the farthest differentiation reached, in a Pentacrinoid 18 days old. There is still no trace of the radials, but the first sacculus and the spicules of the primary tentacle have appeared.

Plate I.

All figures of *Eucidaris metularia* (Lamarck).

Fig. 1. Egg, immediately after fertilization.
- 2. First cleavage.
- 3. Eight cell stage.
- 4. Blastula stage; 6—8 hours after fertilization.
- 5. Gastrula, 24 hours old. Mesenchyme cells proliferating from upper end of archenteron.
- 6. Gastrula, 2 days old. Upper end of archenteron widening to form the mesoderm pouches.
- 7. Embryo, 4 days old, beginning to assume the Pluteus shape; the postoral rods have just begun to form. The suboral cavity distinct. Pigment has begun to appear.
- 8. Young larva, 9 days old.
- 9. Larva, 22 days old. Posterodorsal arms are developing, and the posterior transverse rod has appeared, the small horizontal rod below the stomach.
- 10. Fully formed larva, in side view. Pedicellariæ and spines have appeared. Drawn from a preserved specimen.

Figs. 1—6 × 290; figs. 7—9 × 125; fig. 10 × 40.



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Th. M. del.

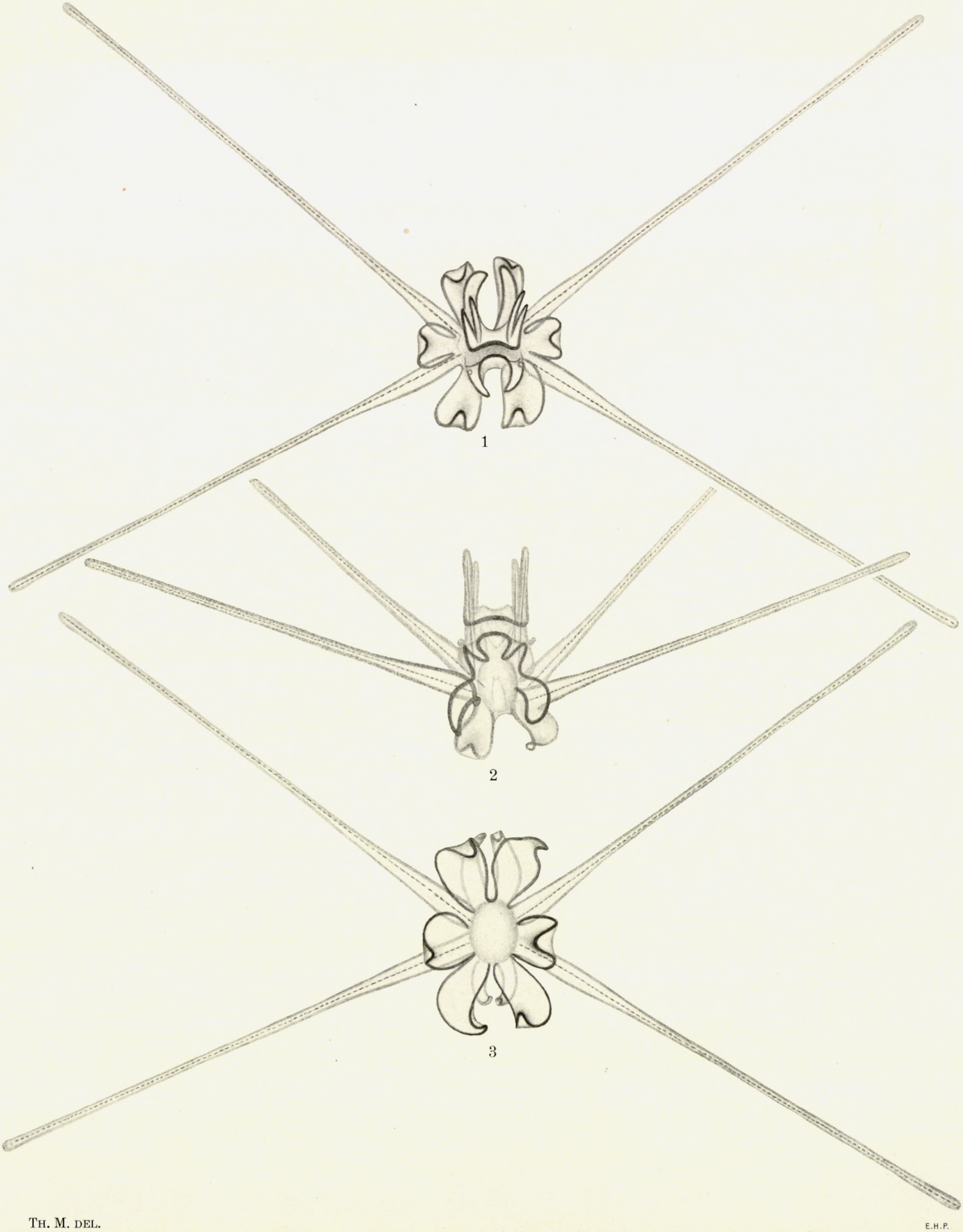
E.H.P

Plate II.

All figures of *Eucidaris metularia* (Lamarck).

Fig. 1. Fully formed larva, seen from above.
- 2. Same, seen from the oral side.
- 3. Same, seen from below.

Drawn from preserved specimens.
The exact age of these larvæ not stated, but they are about 7 weeks old.
All × 40.



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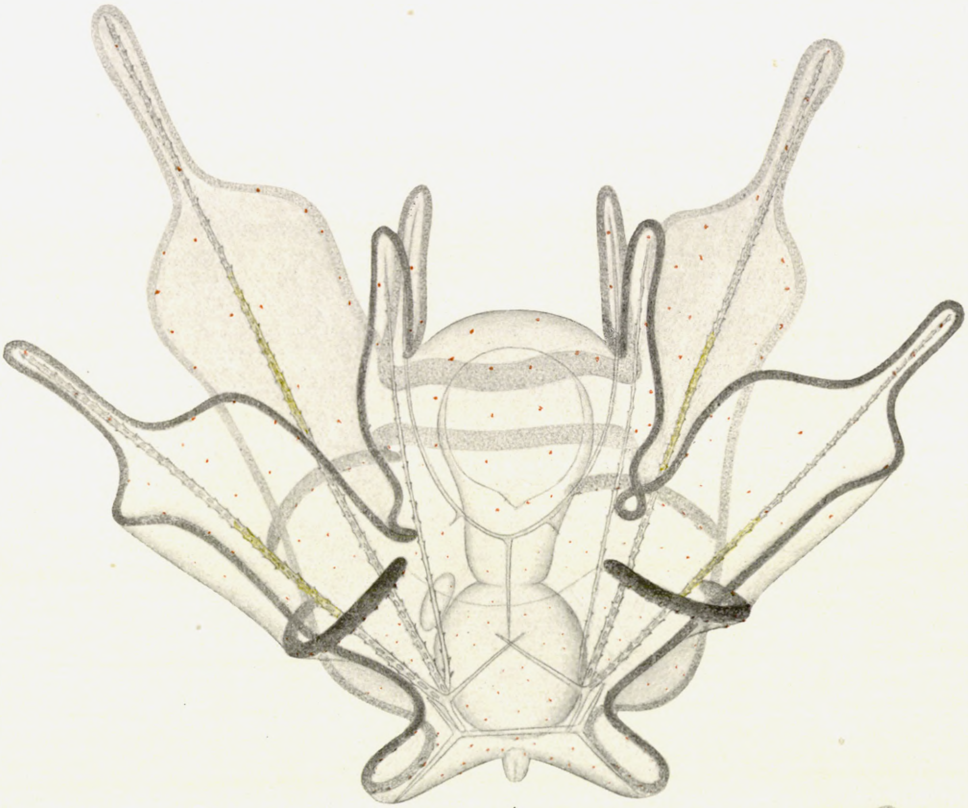
E. H. P.

Plate III.

Temnotrema scillæ (Mazetti).

Fig. 1. Fully formed larva, 15 days old; from the dorsal side. × 115.
- 2. Same, from above. × 100.



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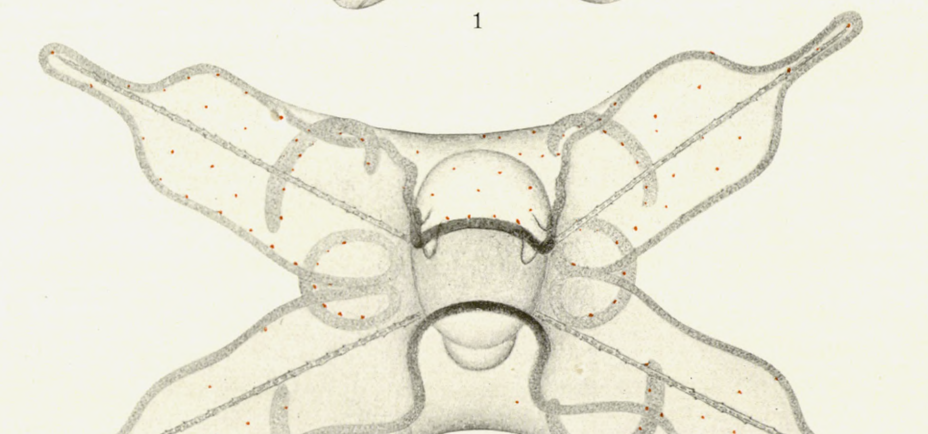

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Th. M. del.

E.H.P.

Plate IV.

Fig. 1. Larva, 15 days old, of *Nudechinus Gravieri* (Koehler), in beginning metamorphosis, from the oral side. $\times$ 145.

- 2. Fully formed larva, 19 days old, of *Tripneustes gratilla* (Linn.) from the oral side. In the posterior end the first pedicellaria has appeared. $\times$ 145.

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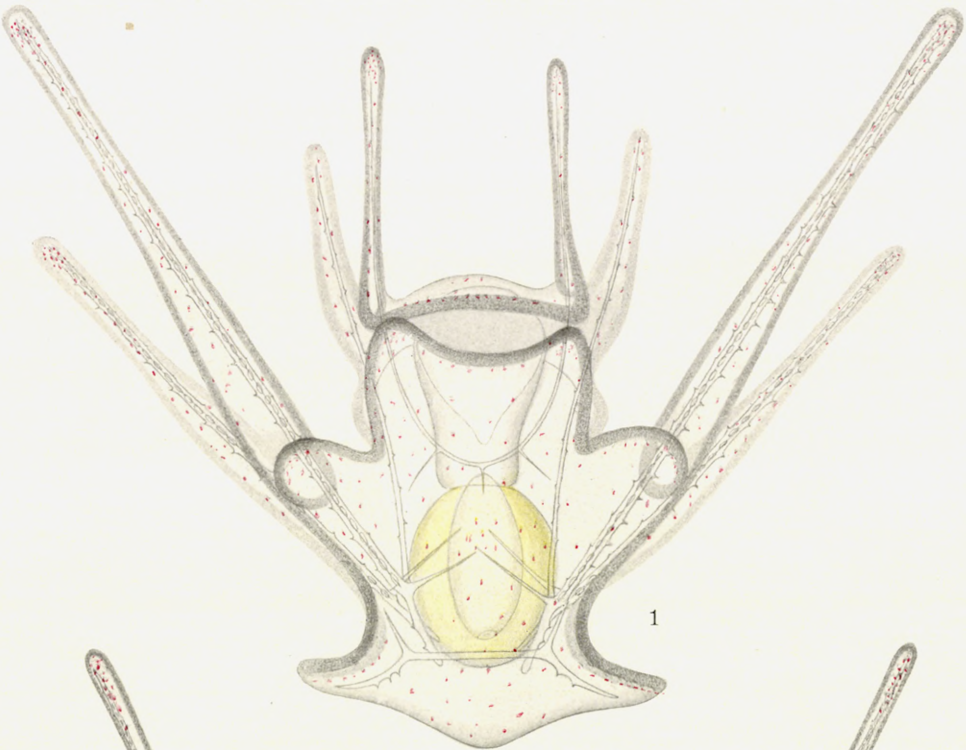
Th. M. del.

E.H.P.

Plate V.

Fig. 1. Fully formed larva of *Echinometra Mathœi* (Blainv.), from the oral side. 28 days old. $\times$ 120.

- 2. Fully formed larva of *Heterocentrotus mammillatus* (Linn.), from the oral side, 24 days old. In the posterior end the first pedicellaria has appeared. $\times$ 105.



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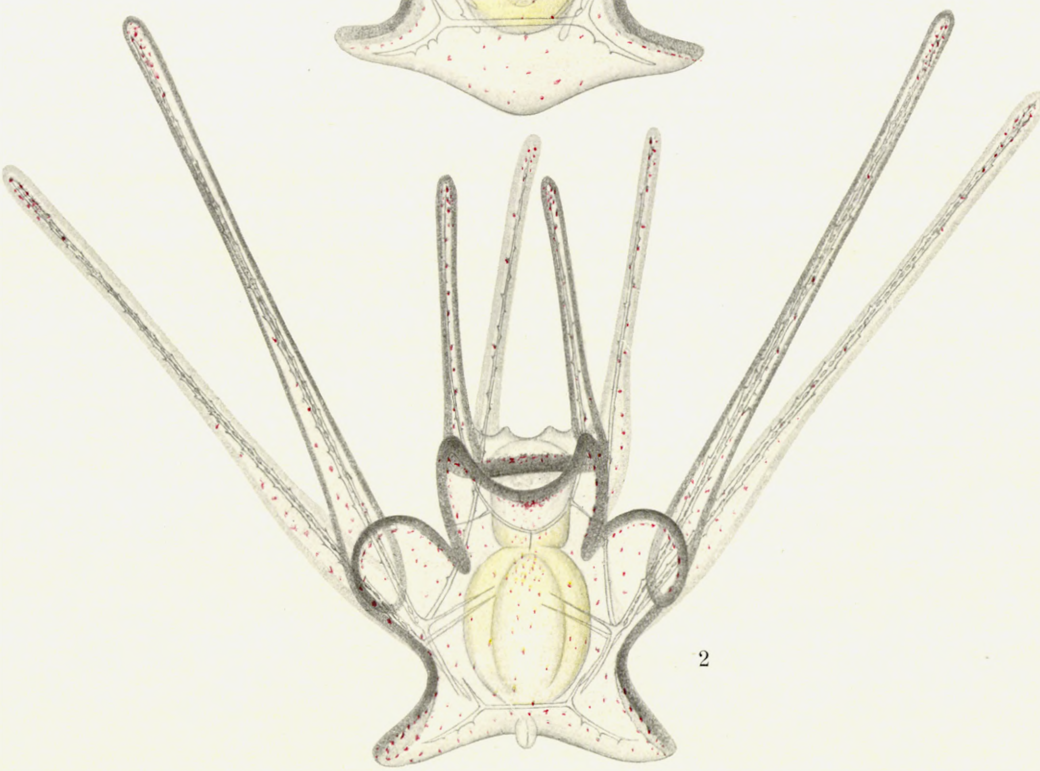

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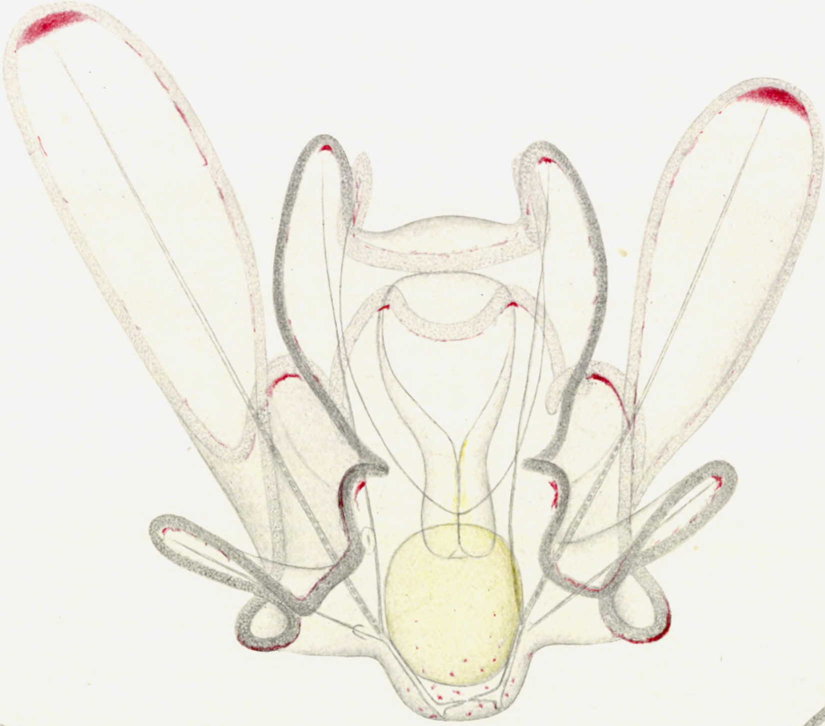
Th. M. del.

E.H.P.

Plate VI.

Fig. 1. Nearly fully formed larva of *Clypeaster humilis* (Leske), from the dorsal side; 14 days old. The posterodorsal arms have not yet reached their full size. The amnion has just appeared. × 110.

- 2. Same, seen from the oral side, a little from behind. The posterodorsal arms more developed, but not full size, which will be like the postoral arms. × 110.



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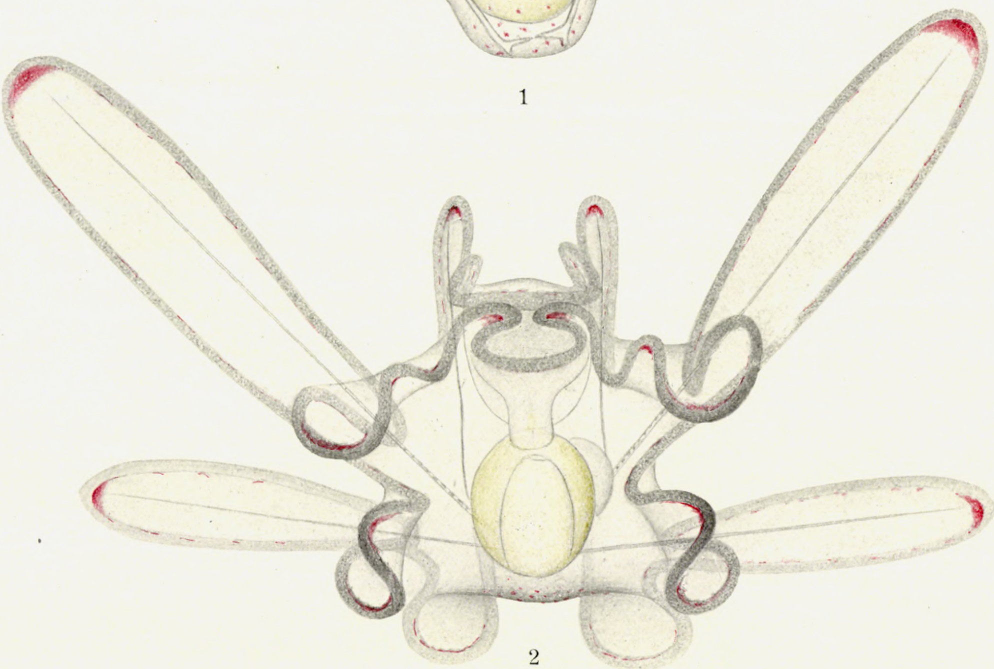

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Th. M. del.

E.H.P.

Plate VII.

Fig. 1. Fully formed larva of *Fibularia craniolaris* (Leske), from the oral side. 19 days old. $\times$ 100.

- 2. Fully formed larva of *Echinodiscus auritus* (Leske), from the oral side. 5 days old. $\times$ 130.

- 3. Fully formed larva of *Lovenia elongata* (Gray), from the oral side. 14 days old. $\times$ 60.

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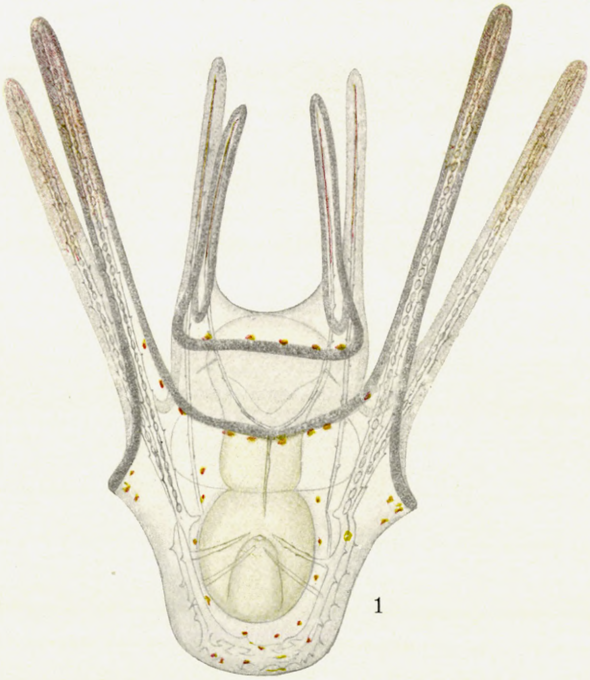

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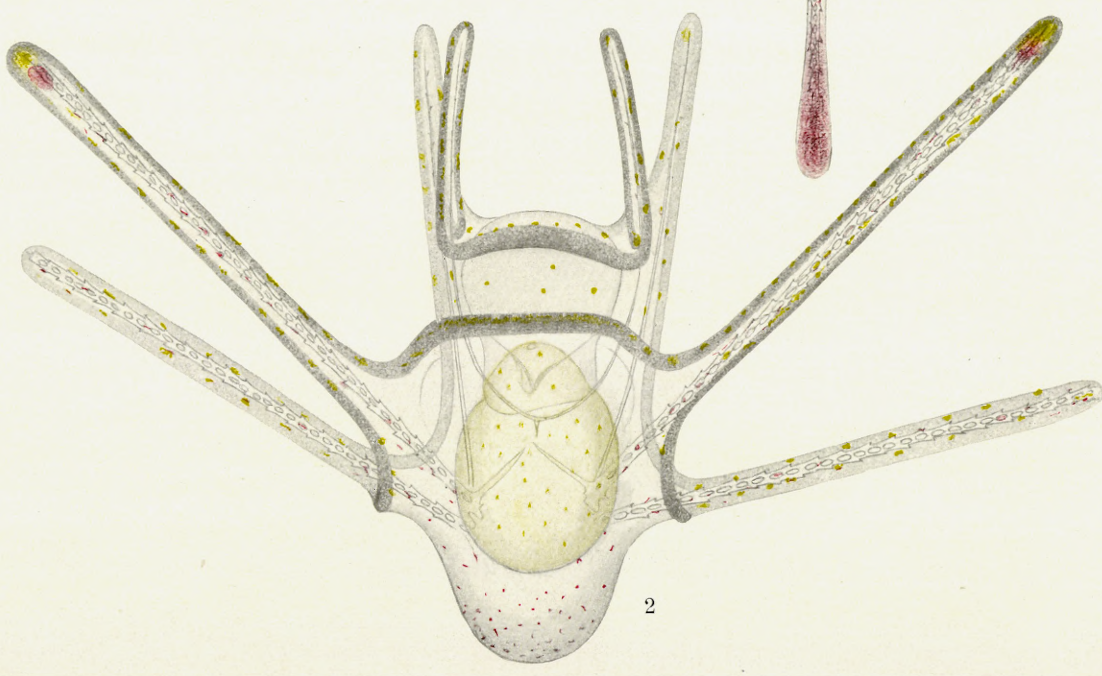

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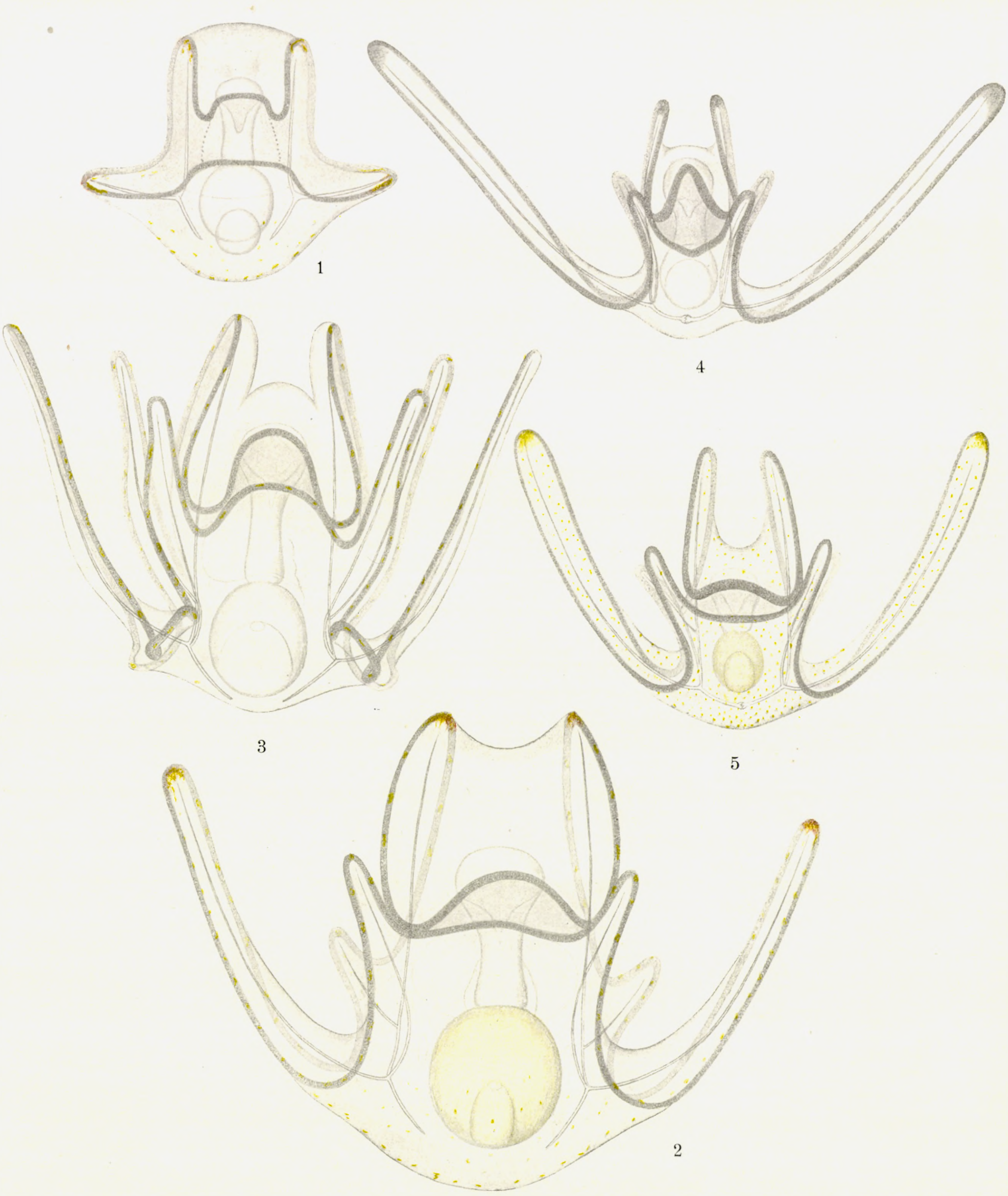
Th. M. del.

E.H.P.

Plate VIII.

Fig. 1. Young larva of *Ophiocoma lineolata* Desjardins (Müll. & Troschel) 6 days old. × 110.
- 2. Same, 18 days old. × 110.
- 3. Fully formed larva of *Ophiocoma lineolata* Desj. (Müll. & Troschel) 5 weeks old; near metamorphosis, the hydrocoel having begun to form lobes. × 80.
- 4. Larva of *Ophiocoma erinaceus* Müll. & Troschel. 5 weeks old. × 80.
- 5. Larva of *Ophiocoma scolopendrina* (Lamarck). 11 days old. × 80.

All from the oral side.



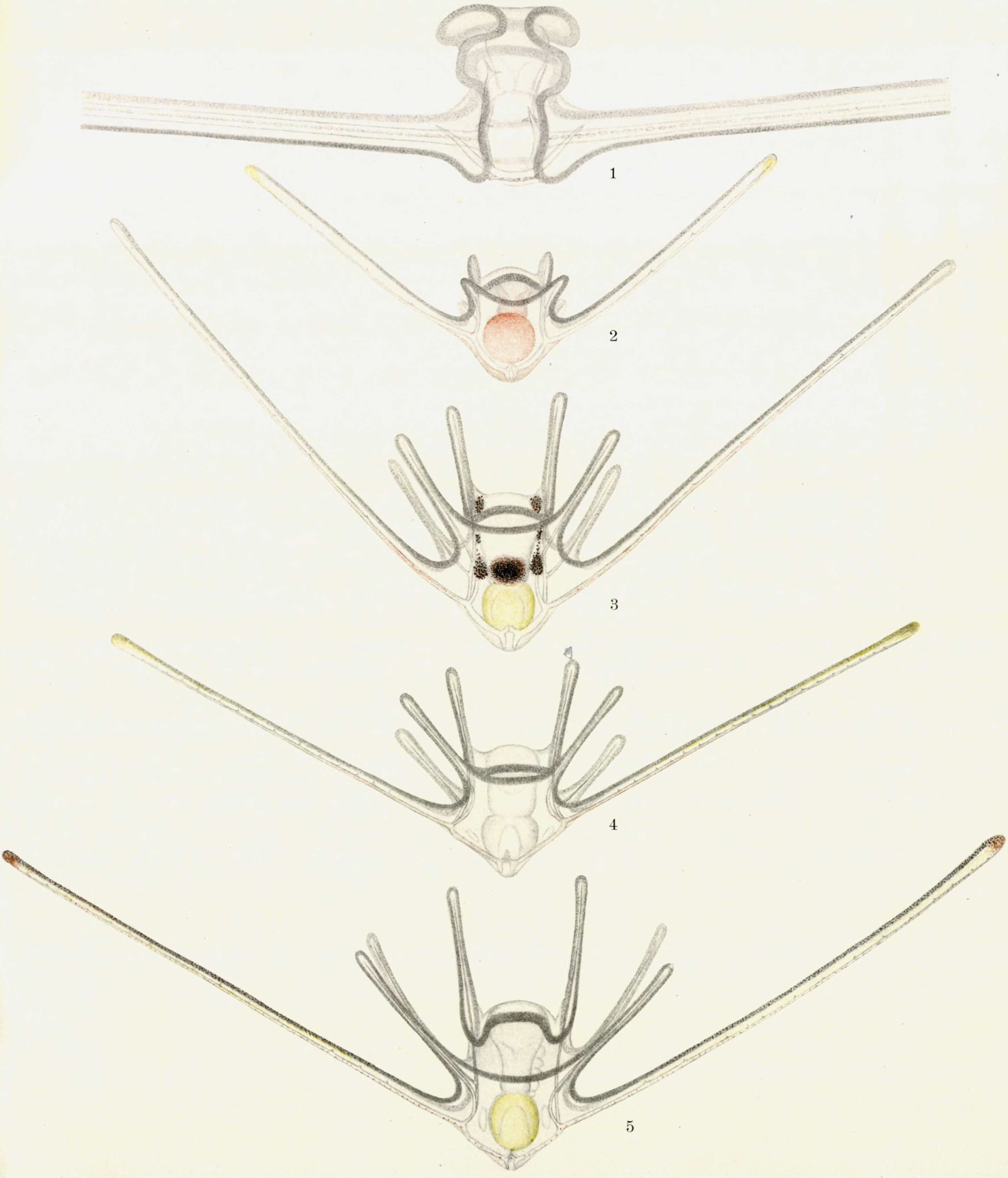
Th. M. del.

E.H.P.

Plate IX.

Fig. 1. Fully formed larva of *Diadema setosum* (Leske), from the dorsal side. 30 days old. From a preserved specimen. × 120.
- 2. Young larva of *Ophiothrix triloba* v. Martens, 4 days old. × 90.
- 3. Fully formed larva of *Ophiothrix triloba* v. Martens, 15 days old. × 90.
- 4. Young larva of *Ophiomaza cacaotica* Lyman, 5 days old. × 90.
- 5. Larva of *Ophiomaza cacaotica* Lyman, 17 days old; in beginning metamorphosis, the hydrocoel having begun to form lobes. × 90.

Figs. 2—5 from the oral side.



Th. M. del.

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Plate X.

Fig. 1. Gastrula of *Temnotrema scillæ* (Mazetti), 22 hours old. The mesoderm pouches beginning to form from the upper end of the archenteron. × 260.
- 2. Larva of *Astropecten polyacanthus* Müll. & Troschel, 3 days old; from the oral side. In beginning metamorphosis. × 80.
- 3. Larva of *Astropecten velitaris* v. Martens, 4 days old; from the dorsal side. In beginning metamorphosis. × 80.
- 4. Larva of *Asterope carinifera* (Lamarck), 30 days old; from the oral side. In beginning metamorphosis. × 80.
- 5. Larva of *Astropecten polyacanthus* Müll. & Troschel, 5 days old; in side view. In beginning metamorphosis. × 50.
- 6. Young larva of *Synaptula reciprocans* (Forskål), 4 days old; from the oral side. × 110.
- 7. Larva of *Synaptula vittata* (Forskål), 4 days old; from the oral side. × 110.

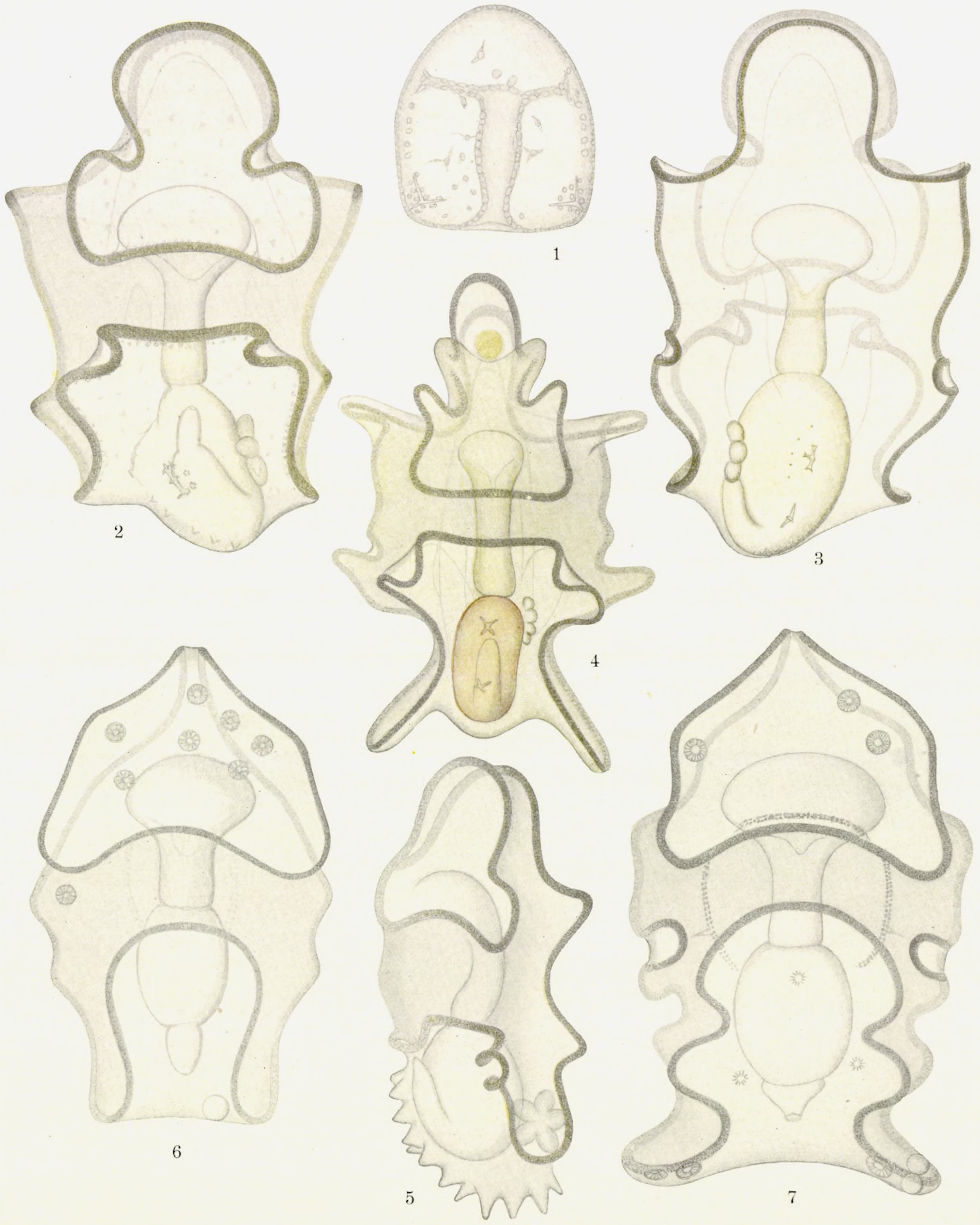
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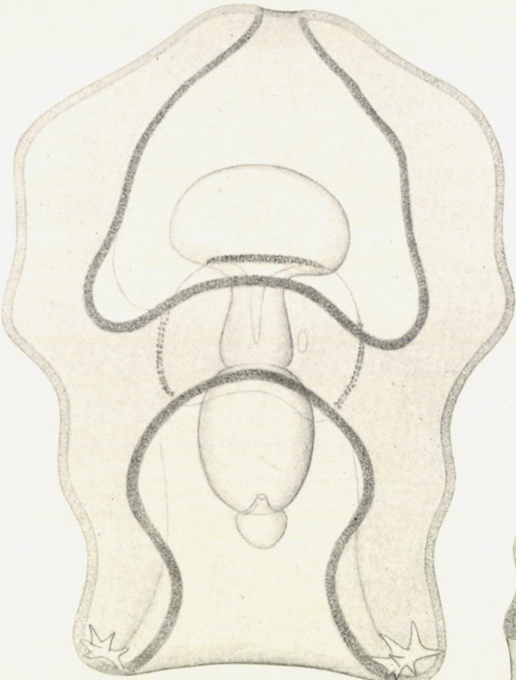
Plate XI.

Fig. 1. Young larva of *Stichopus variegatus* Semper, 7 days old; from the oral side. × 200.
- 2. Larva of same, nearly fully formed, from the oral side. × 130.
- 3. Larva of same, from the dorsal side. Showing double hydrocoel. × 130.
- 4. Larva of same, from the dorsal side; in beginning metamorphosis. × 130.
- 5. Young Holothurian of *Stichopus variegatus* Semper, just metamorphosed. × 130.
- 6. Young larva of *Synaptula vittata* (Forskål), in side view; 11 days old. × 100.

Figs. 2—5 drawn from preserved specimens; exact age unknown.



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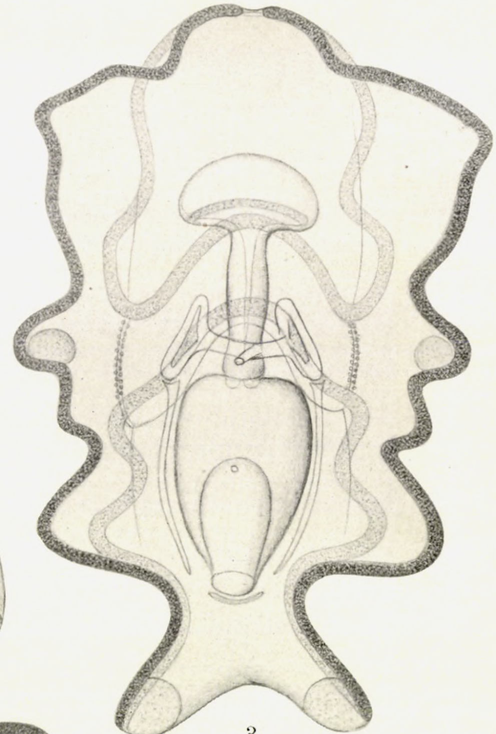

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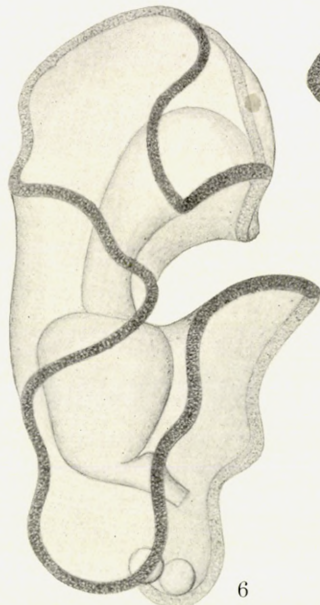

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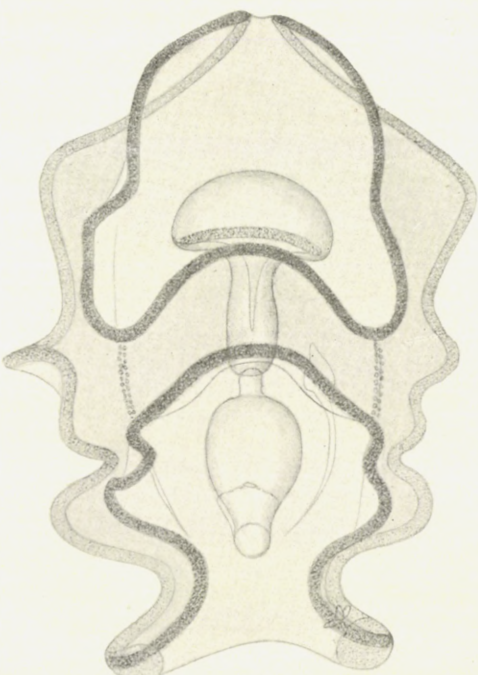

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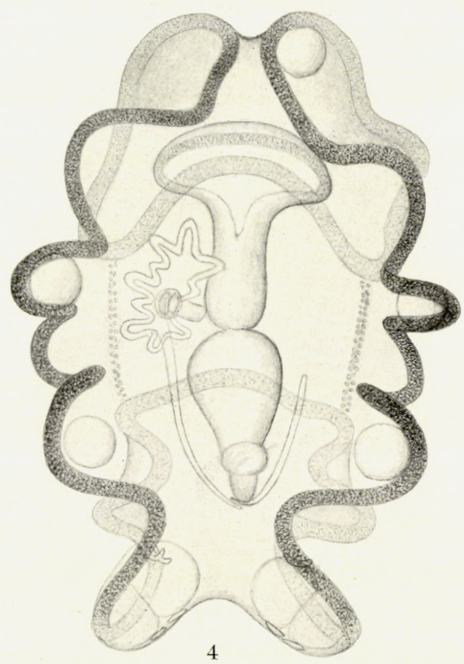

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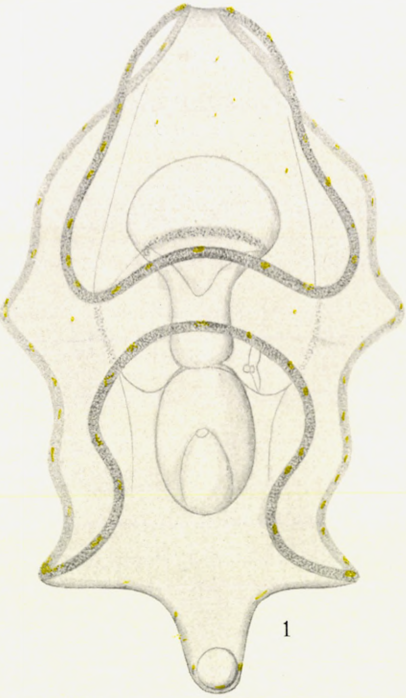
Th. M. del.

E. H. P.

Plate XII.

Fig. 1. Larva of *Holothuria scabra* Jäger, 6 days old. × 80.
- 2. Same, 18 days old; in beginning metamorphosis. Abnormally with a right hydrocoel. × 80.
- 3. Larva of *Holothuria arenicola* Semper, var. *Boutani* Hérouard; 10 days old. × 80.
- 4. Same in beginning metamorphosis; 26 days old. × 80.
- 5. Larva of *Holothuria (Bohadschia) marmorata* Jäger. 11 days old. × 110.
- 6. Same, 10 days old. (From another culture than the larva represented in fig. 5). × 80.

All from the oral side.



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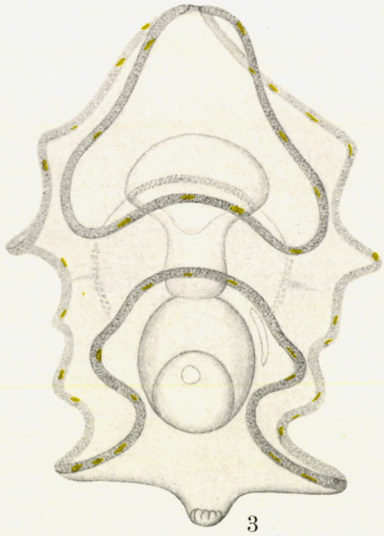

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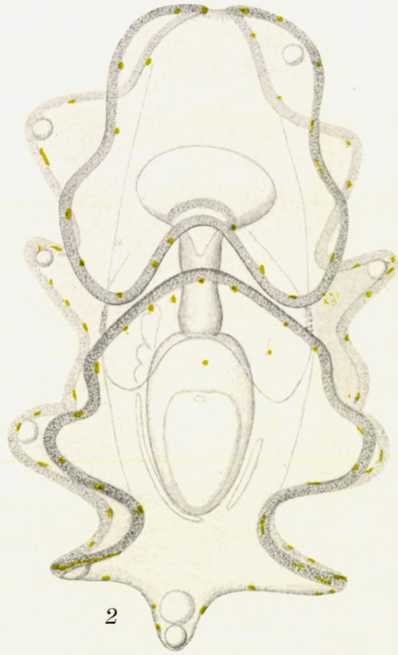

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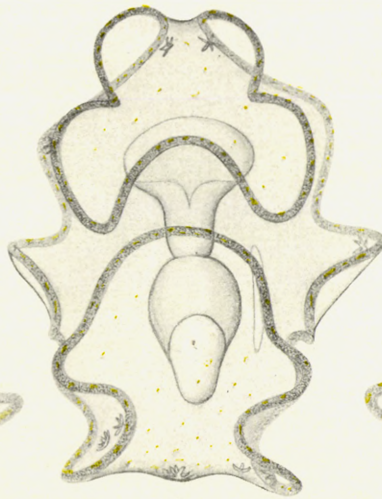

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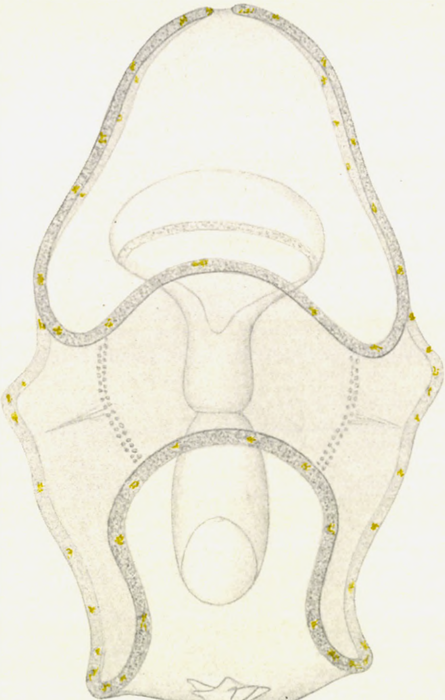
Th. M. del.

E.H.P.

Plate XIII.

Fig. 1. Young larva of *Actinopyga serratidens* Pearson, 10 days old; from the oral side. × 125.
- 2. Larva of same, 3 weeks old; from the oral side. In beginning metamorphosis. × 100.
- 3. Young Holothurian of *Actinopyga serratidens* Pearson, newly metamorphosed. 26 days old. × 125.
- 4. Larva of *Holothuria mauritiana* Quoy & Gaimard, Var. 8 days old. From the oral side. × 90.
- 5. Larva of *Holothuria spinifera* Théel, 8 days old; from the oral side. × 200.

PL. XIII



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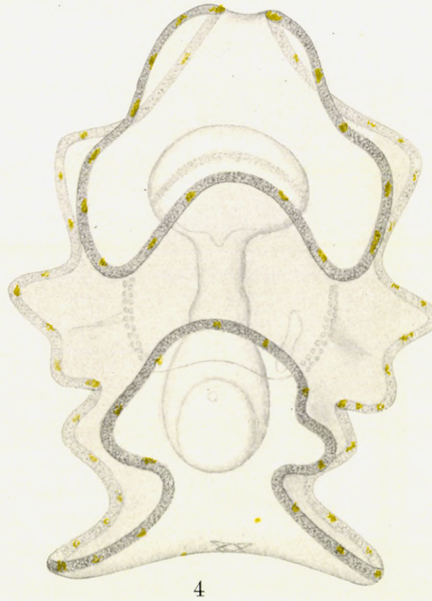

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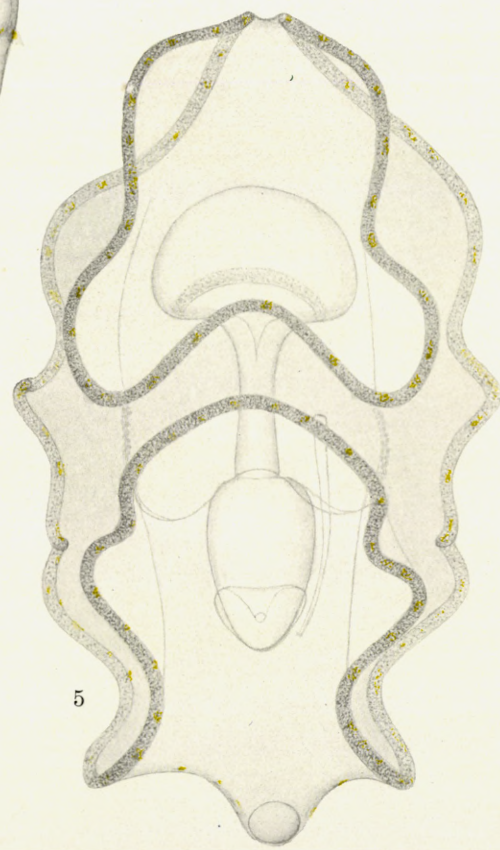

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TH. M. DEL.

E.H.P.

Plate XIV.

Fig. 1. Pentacrinoid, 3 weeks old, of *Tropiometra Audouini* A. H. Clark. × 100.
- 2. Calyx of another Pentacrinoid of *Tropiometra Audouini,* same age; showing anal plate. × 200.
- 3—4. Embryos of *Lamprometra Klunzingeri* (Hartlaub), 36 hours old, showing development stages of calyx-plates and stalk. × 300.
- 5—7. Young Pentacrinoids of *Lamprometra Klunzingeri,* figs. 5—6 five days old, fig. 7 six days old. × 125.
- 8. Calyx of Pentacrinoid, 18 days old, of *Lamprometra Klunzingeri,* showing the first sacculus and spicules in the primary tentacle, but still no trace of the radial. × 200.

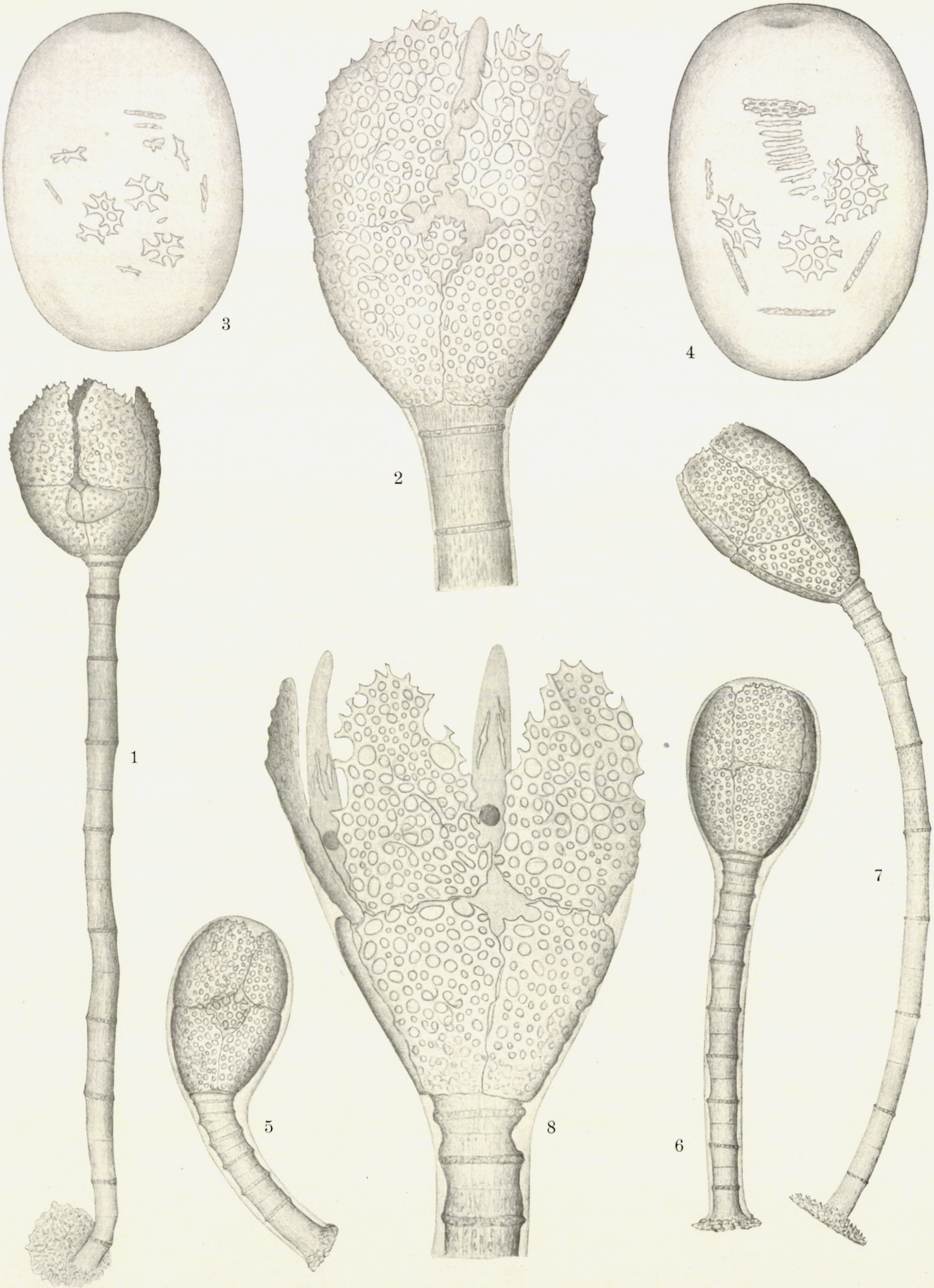

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Plate XV.

All figures of *Lamprometra Klunzingeri* A. H. Clark. All × 300.

Fig. 1—2. The two first cleavage stages, lying within the thorny egg-membrane; 2 hours old. The nuclei very indistinct, the stain penetrating only with difficulty the egg-membrane.

- 3. Section through embryo 4 hours old, still within the egg-membrane. Shows the blastocoel cavity wholly occupied by cells derived from the ectoderm.

- 4. Section through embryo 10 hours old, still within the egg-membrane. The blastocoel cavity quite filled by numerous mesenchyme cells. No gastrula invagination. Ectoderm not distinctly limited from mesenchyme cells.

- 5. Longitudinal section through a free-swimming embryo, 15 hours old. The gastral cavity has been formed.

- 6. Transverse section of embryo, 15 hours old, still within the egg-membrane. Gastral cavity distinct. The thickening of the ectoderm is either the beginning formation of the vestibulum or of the sucking disk; the impossibility of orientation by sectioning prevents deciding which of the two alternatives is the correct.

- 7. Longitudinal section of an embryo 22 hours old, showing the division of the gastral cavity into an upper and lower part, the former the entero-hydrocoel, the latter the coelomic vesicle.

- 8. Longitudinal section through an embryo, $1^1/_2$ days old, with the vestibulum formed. The small cavity below the vestibulum is the stomach, the other cavity the coelomic vesicle, dividing into a right and a left part.

- 9. Transverse section through embryo $1^1/_2$ days old, showing vestibulum.

- 10. Longitudinal section through an embryo 3 days old. The vestibulum beginning to close. Beginning formation of the chambered organ.

Th. M. del.

E.H.P.

Det Kongelige Danske Videnskabernes Selskab.

Skrifter, naturvidenskabelig og mathematisk Afdeling.

9. Række.

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Det Kongelige Danske Videnskabernes Selskab.

Skrifter, naturvidenskabelig og mathematisk Afdeling.

9. Række.

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